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Worldwide tests of generic attractants, a promising tool for early detection of non-native cerambycid species

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Abstract

A large proportion of the insects which have invaded new regions and countries are emerging species, being found for the first time outside their native range. Being able to detect such species upon arrival at ports of entry before they establish in non-native countries is an urgent challenge. The deployment of traps baited with broad-spectrum semiochemical lures at ports-of-entry and other high-risk sites could be one such early detection tool. Rapid progress in the identification of semiochemicals for cerambycid beetles during the last 15 years has revealed that aggregation-sex pheromones and sex pheromones are often conserved at global levels for genera, tribes or subfamilies of the Cerambycidae. This possibly allows the development of generic attractants which attract multiple species simultaneously, especially when such

pheromones are combined into blends. Here, we present the results of a worldwide field trial programme conducted during 2018–2021, using traps baited with a standardised 8-pheromone blend, usually complemented with plant volatiles. A total of 1308 traps were deployed at 302 sites covering simultaneously or sequentially 13 European countries, 10 Chinese provinces and some regions of the USA, Canada, Australia, Russia (Siberia) and the Caribbean (Martinique). We intended to test the following hypotheses: 1) if a species is regularly trapped in significant numbers by the blend on a continent, it increases the probability that it can be detected when it arrives in other countries/continents and 2) if the blend exerts an effective, generic attraction to multiple species, it is likely that previously unknown and unexpected species can be captured due to the high degree of conservation of pheromone structures within related taxa. A total of 78,321 longhorned beetles were trapped, representing 376 species from eight subfamilies, with 84 species captured in numbers greater than 50 individuals. Captures comprised 60 tribes, with 10 tribes including more than nine species trapped on different continents. Some invasive species were captured in both the native and invaded continents. This demonstrates the potential of multipheromone lures as effective tools for the detection of 'unexpected' cerambycid invaders, accidentally translocated outside their native ranges. Adding new pheromones with analogous well-conserved motifs is discussed, as well as the limitations of using such blends, especially for some cerambycid taxa which may be more attracted by the trap colour or other characteristics rather than to the chemical blend.

Keywords

Cerambycidae, early detection, Holarctic, invasion, multi-pheromone blend, pheromone trapping

Introduction

During the last several decades, the unprecedented development of worldwide trade has resulted in increasing translocation and establishment of non-native insects outside their native ranges, with little evidence of saturation (Seebens et al. 2017, 2021). Insect herbivores, accidentally introduced as plant contaminants, appear to be mainly responsible for this sharp increase, at least in Europe (Roques 2010; Pergl et al. 2017). Amongst these non-native herbivores, species associated with woody plants largely dominate, accounting for 76.5% of all herbivore species newly recorded in Europe from 2000 to 2014, while species of importance to agricultural plants and products are a minority (Roques et al. 2016). The increased extent of trade in ornamental plants has been suggested as a major driver of this increase (Liebhold et al. 2012; Eschen et al. 2014; Essl et al. 2015; Roques et al. 2020). Additionally, wood packaging material (e.g. pallets, crating, dunnage) transported with international cargo shipments represents another significant pathway for introduction of non-native phloem- and wood-boring insects (Aukema et al. 2010; Haack et al. 2014; Lovett et al. 2016). An average of 6.1 non-native insect species attacking woody plants became newly established in Europe per year from 2000–2019, compared to 2.4 cases per year from 1950–1970 (Roques et al. 2020). Similar trends were observed in North America (Aukema et al. 2010), New Zealand (Brockerhoff and Liebhold 2017) and at a slower rate in China (Roques et al. 2020).

Another key attribute of this recently-arrived, non-native entomofauna is the increasing presence of "emerging" species, which have not been reported previously as invaders and are not considered to be pests in their native ranges. Arrival of these species probably results from evolving changes in trade routes and imported goods, which leads to accessibility to new pools of species (Seebens et al. 2018). For example, the emerald ash borer, *Agrilus planipennis* Fairmaire, was not considered a significant pest until it invaded North America, where it has caused massive damage (Dang et al. 2022). The same is true for a number of other xylophagous cerambycid beetle species which have recently invaded Europe, such as the Asian mulberry longhorned beetle, *Xylotrechus chinensis* (Chevrolat) (Sarto i Monteys and Torras i Tutusaus 2018), the round-headed apple-tree borer, *Saperda candida* Fabricius (Nolte and Krieger 2008) and the Asian redneck longhorned beetle *Aromia bungii* (Faldermann) (Russo et al. 2020). At first, such species were typically not subject to regulatory measures or strict phytosanitary inspections at borders because their invasive potential had not been recognised. For example, only seven of the 117 non-native insect species that infest woody plants that established in Europe during the period 1995–2012 had been intercepted in such inspections (Eschen et al. 2015). In Australia, 61 of the 135 non-native species established in forests during the period 2003–2016 had never been intercepted, despite relatively intensive border controls (Nahrung and Carnegie 2021). Therefore, the development of new strategies to detect such unanticipated and unregulated species as early as possible is essential to implement rapid and effective eradication or containment measures (Nahrung et al. 2023).

Deployment of traps baited with broad-spectrum semiochemical lures at ports-of-entry (Brockerhoff et al. 2006; Rassati et al. 2014, 2015a; Hoch et al. 2020) or other high-risk sites (e.g. urban wood-waste landfills and industrial sites, Rassati et al. 2015b; Rabaglia et al. 2019) could be one such early detection tool. Given the difficulty of predicting which species may arrive and in what numbers (i.e. propagule pressure), such lures should be efficient even at low population densities and should ideally attract multiple species from different taxa (family, subfamily, tribe). Combining pheromones of several species into blends could be expected to result in such a generic attraction when antagonistic effects amongst blend components are relatively minor, for example, reduced attraction of relatively few species, such that the net effect of blending multiple components is an increase in the number of target taxa detected. The addition of plant volatiles, acting as kairomones, may further enhance the attraction. For instance, a pine specialist, *Monochamus galloprovincialis* (Olivier), was significantly more attracted when its pheromone, monochamol, was combined with volatiles from its pine hosts (Alvarez et al. 2016). Similarly, ethanol had a synergist effect on the capture of species related to broadleaved trees in Eurasia (*Phymatodes testaceus* [L.]; Sweeney et al. 2014; Fan et al. 2019) and in southern USA (Miller et al. 2017). However, the addition of plant volatiles did not affect, either positively or negatively, the captures of several other cerambycid species (Fan et al. 2019). Overall, relationships between host volatiles and cerambycids are probably more dependent on the exploited host and less on insect taxonomy. Potential for using blended lures for detection would be further

enhanced if each component of the blend was attractive to multiple related species, i.e. a pheromone or kairomone shared by species within a genus or tribe as occurs in the longhorned beetle family Cerambycidae.

This large family of Coleoptera includes between 34,000 and 38,000 described species (Rossa and Goczał 2021; Tavakilian and Chevillotte 2022). Although recent molecular studies using a multigene approach revealed that the phylogeny at the upper taxonomic levels is not completely resolved and still under debate (Lee and Lee 2020; Nie et al. 2020), Tavakilian and Chevillotte (2022) recognised 13 subfamilies. The subfamily Lamiinae is by far the most diverse with more than 21,000 species, 3,002 genera and 86 tribes, followed by Cerambycinae (> 12,000 species, 1,848 genera, and 119 tribes), Lepturinae (> 1,830 species, 232 genera, 11 tribes), Prioninae (> 1,250 species, 311 genera, 26 tribes) and Spondylidinae (> 150 species, 32 genera, seven tribes); other subfamilies are smaller and much less diverse. Cerambycid larvae of many species develop as endophytic borers concealed beneath the bark of woody plants or, much less frequently, within herbaceous plants. This cryptic lifestyle, coupled with the usual long duration of the hidden larval stages, facilitates the transport of these insects around the world in logs and wooden packing materials (Eyre and Haack 2017), but also via trade in living plants if the plants have a sufficiently large diameter. For example, larvae of the citrus longhorned beetle, *Anoplophora chinensis* (Forster), were detected in Japanese maples, *Acer palmatum* Thunb., shipped to Europe (Eschen et al. 2015). Thus, a steadily increasing number of cerambycid species have become globally important as invasive forest and orchard pests (Venette and Hutchison 2021).

Recent advances in the chemical ecology of cerambycids and, particularly, the identification of volatile pheromones that act as long-range attractants, have provided new tools and opportunities for monitoring invasive woodborers. In total, pheromones or likely pheromones have been identified for more than 400 cerambycid species worldwide (Millar and Hanks 2017). Furthermore, field experiments have shown that these pheromones can be deployed in blends, with a potential generic attraction for both native and non-native species (Hanks et al. 2012; Hanks and Millar 2016; Hanks et al. 2018; Fan et al. 2019; Flaherty et al. 2019; Rassati et al. 2019). Currently, the aggregated data suggest that species in the subfamilies Cerambycinae, Lamiinae and Spondylidinae use male-produced aggregation-sex pheromones to attract both sexes, whereas species in the subfamilies Prioninae and Lepturinae use female-produced pheromones that attract only males (Hanks and Millar 2016). This research has revealed striking patterns in pheromone chemistry. Pheromone components are frequently highly conserved amongst species within genera, tribes and even at the subfamily level (Hanks and Millar 2013, 2016). For example, in the subfamily Lamiinae, hydroxyethers are used as aggregation-sex pheromones by many species native to different continents. Thus, 2-(undecyloxy)ethanol, or monochamol, is a pheromone component shared by European, North American and Asian species in the genus *Monochamus*, all of which vector the pine wood nematode (*Bursaphelenchus xylophilus* [Steiner & Buhrer]) (Pajares et al. 2010; Hanks and Millar 2016; Boone et al. 2018; Lee et al. 2018). In addition, field trials in southern China showed that four lamiine species in genera other

than *Monochamus* were attracted to monochamol (Wickham et al. 2014). A number of other compounds are widely shared amongst species within a given subfamily in different world regions. For example, terpenoids such as fuscumol ([*E*]-6,10-dimethyl-5,9-undecadien-2-ol) and its acetate, are aggregation sex-pheromone components for many species in the subfamily Spondylidinae and Laminae (Mitchell et al. 2011; Hanks and Millar 2016). In contrast, many species in the subfamily Cerambycinae from different continents utilise short-chain (6–10 carbon) hydroxyketones, such as 3-hydroxyalkan-2-ones and 2-hydroxyalkan-3-ones and the corresponding *syn-* and *anti*-2,3-alkanediols as aggregation-sex pheromones (Hanks and Millar 2016). Prionic acid ([3*R*,5*S*]-3,5-dimethyldodecanoic acid) similarly appears to be shared as a sex pheromone by several genera of the subfamily Prioninae on different continents (Barbour et al. 2011; Wickham et al. 2016a). This sharing of pheromone components by species in different world regions suggests that traps baited with these compounds have a good chance of detecting non-native, phylogenetically-related invaders that are introduced to another continent. Moreover, combining several of these pheromone components in a single blend has the potential to detect a broader range of species.

During the last 10 years, the generic effectiveness of such multi-component blends has been tested on different continents, but using different pheromone combinations, either alone or in combination with kairomones, such as ethanol and α-pinene (e.g. Miller et al. 2017; Fan et al. 2019). In Illinois, USA, Hanks et al. (2012) first tested a six-component blend, which included racemic 3-hydroxyhexan-2-one, *syn-* and *anti*-2,3-hexanediols, fuscumol, fuscumol acetate, monochamol and racemic 2-methylbutan-1-ol. Ten cerambycid species were caught in significant numbers in these trials, including four species in the subfamily Cerambycinae and six in the subfamily Lamiinae. Hanks et al. (2018) then tested this 6-component blend at a larger scale in several regions of the USA, adding both prionic acid and plant volatiles to the traps. The pheromone blend attracted about twice as many species as any of the individual components and the species attracted by the blend included three subfamilies, whereas individual components attracted species within only one subfamily. The inclusion of prionic acid also resulted in the additional captures of *Prionus* spp. which were not trapped by the previous six-pheromone blend. In a natural reserve in Yunnan (China), Wickham et al. (2021) trapped 71 species with another generic lure comprised of six components, three of which were the same as those used in the USA (*anti*-2,3-hexanediol, racemic 3-hydroxyhexan-2-one and monochamol). In France, using an 8-pheromone blend consisting of the same compounds as Hanks et al. (2018) to which was added geranylacetone targeting Spondylininae (Halloran et al. 2018), Fan et al. (2019) trapped 118 species, of which 114 were native species that represented 48% of the French cerambycid fauna. Trapping more than 50% of the species in 25 of the 41 cerambycid tribes present in the country indicates a considerable generic attraction of this 8-pheromone blend, significantly higher than an earlier trial which tested a blend of four pheromones. By contrast, unbaited control traps deployed in the same French sites caught very few species. Other trials of potentially generic blends, including fewer or different

compounds, were carried out in Russia (Sweeney et al. 2014), Australia (Hayes et al. 2016), Brazil (Silva et al. 2017), Poland, Italy and Canada (Flaherty et al. 2019; Rassati et al. 2019, 2021). Results from Australia differed from those reported in other continents because the tested blend attracted no more species than 3-hydroxyhexan-2-one alone (Hayes et al. 2016).

When using multi-pheromone blends, antagonistic effects might occur with either pheromone components or host plant volatiles (e.g. Hanks et al. 2018; Rassati et al. 2021). The North American species *Neoclytus acuminatus acuminatus* (F.), for example, was strongly attracted by *syn*-2,3-hexanediol, but the addition of racemic 3-hydroxyhexan-2-one to the latter pheromone interrupted attraction (Rassati et al. 2021). Addition of host plant volatiles, such as ethanol, significantly enhanced attraction of some cerambycid species (Sweeney et al. 2014; Miller et al. 2017; Hanks et al. 2018), but, with the exception of *P. testaceus*, had little effect on catch of cerambycid species in other studies (Fan et al. 2019). However, as long as inhibition did not completely prevent attraction, one trap with a multi-pheromone lure may still be somewhat more cost-effective than deploying multiple traps baited with individual lures. This can be assessed by a cost-benefit analysis, i.e. estimating the labour and materials costs of deploying and servicing a network of traps baited with single components, versus the costs of deploying and servicing a single trap baited with a blend of the same components.

Results of these different experiments on various continents stimulated us to propose a worldwide trapping programme using a standardised 'generic' 8-pheromone blend in all countries/trapping sites. The blend included the following compounds known to be widely shared amongst cerambycids of related taxa: fuscumol, fuscumol acetate, monochamol, geranylacetone, *anti*-2,3-hexanediol, 3-hydroxyhexan-2-one (C6-ketol), 2-methylbutan-1-ol and prionic acid. The programme relied on the following hypotheses: 1) if a species is attracted in significant numbers by the blend in a region, it increases the probability that it can be detected when it arrives at ports-of-entry in other regions and 2) if the blend exerts an effective, generic attraction to multiple species, it is likely that previously unknown and unexpected species can be captured due to the high degree of conservation of pheromone structures within related taxa, as described above. Our overarching objective was to build a global database of cerambycid species trapped by the 8-pheromone blend. To this end, field trials were conducted during 2018–2021 using operational protocols that were standardised as much as possible at all sites worldwide to cover simultaneously or sequentially 13 European countries, 10 Chinese provinces and some regions of the USA, Canada, Australia, Russia (Siberia) and the Caribbean. Over the course of the study, we also tested the possibility of adding new compounds to enlarge the pool of species trapped. Therefore, in 2020, two additional pheromones, the sex-aggregation pheromones trichoferone (a hydroxyketone pheromone of the velvet longhorned beetle, *Trichoferus campestris* (Faldermann) (Ray et al. 2019) and (*E*)-2-*cis*-6,7-epoxynonenal, the pheromone of the invasive species *A. bungii* (Xu et al. 2017), were added to the original 8-pheromone blend and tested in France and China. In addition, ethanol and α-pinene were included in most trials as synergists for some cerambycids.

Materials and methods

Study sites

The successive or parallel development of three European research projects (HOMED, MULTITRAP, SAMFIX) and two French projects (CANOPEE, PORTRAP) during 2018–2021 allowed us to carry out field trials at 302 sites distributed as follows: 244 in Europe (164 in France, 22 in Italy, 13 in Spain and Switzerland, 6 in Portugal, 5 in Austria and England, 4 in Greece and Slovenia, 3 in the Netherlands, 2 in Bulgaria and the Czech Republic and 1 in Sweden), 38 in Asia (35 in China and three in Siberia, Russia), 11 in North America (10 in the USA and one in Canada), five in the Caribbean (Martinique) and four in Australia (see Table 1 and Suppl. material 1 for details per country, coordinates and the relevant research project). A total of 1308 traps were deployed in stands of broad-leaved and/or coniferous trees in natural or managed environments, but also within and nearby potential ports-of-entry (maritime and fluvial ports, airports, national markets). Experiments in these latter sites usually included two traps placed on trees planted within the port and two traps placed in woody areas located within a 1 km-radius from the port, except in 2019 when a larger experiment was carried out (see below).

In 2018, trials were limited to four European countries (Austria, England, France, the Netherlands), including 41 sites with 143 traps. The 2019 trials were much more extensive and involved 12 European countries (the four from 2018, supplemented by Bulgaria, the Czech Republic, Greece, Italy, Portugal, Spain, Sweden and Switzerland), five provinces of China (Beijing, Hebei, Liaoning, Yunnan and Zhejiang), two States of the USA (Michigan and Ohio) and one site in Canada (Nova Scotia), resulting in a total of 79 sites and 626 traps. These 2019 trials included a large trapping programme targeting semi-urban forests located close to ports-of-entry in Europe, USA and Canada where 16 (Czech Republic, Portugal, Sweden) or 32 traps (France, Italy, Nova Scotia, Ohio, Switzerland) were deployed at each target site. The 2020 trials were substantially impacted by the COVID-19 pandemic, but were carried out for at least a part of the spring–summer season in six European countries (France, Greece, Italy, Portugal, Spain and Switzerland), eight provinces of China (those of 2019, except Beijing, to which were added Hunan, Inner Mongolia, Jiangxi and Shandong) and extended to Australia (New South Wales) and the Caribbean (Martinique), resulting in a total of 78 sites and 256 traps. The 2021 trials were deployed in the same countries as in 2020, supplemented by an additional European country (Slovenia), Russia (Siberia) and an additional province of China (Gansu), resulting in a total of 104 sites and 283 traps.

Trapping protocol and 8-pheromone blend

Trials at all sites used either multifunnel or cross-vane panel traps supplied by different companies depending on the country (Econex, Spain; ChemTica Internacional, S.A., Heredia, Costa Rica; Alpha Scents Inc., West Linn, Oregon, USA). Cross-vane traps used in Italy (Colli Euganei area) in 2019 were hand-made (see Cavaletto et al. 2021 for

details). Black traps were generally deployed, but other colours were also used in France, Italy, Nova Scotia, Ohio and Switzerland (see Table 1). To improve trapping efficiency, all traps were coated with Fluon (AGC Chemicals Europe Ltd., Thornton Cleveleys, UK) diluted in 1:6 in water (Graham et al. 2010). In forests, traps were usually hung from tree branches or between two trees in the lower canopy, at ~ 3–5 m high. Exceptions are some of the countries involved in the 2019 trapping programme targeting semi-urban forests (i.e. Czech Republic, France, Canada, Italy, Portugal, Sweden, Switzerland and the USA) where traps were placed both in the understory and in the upper canopy (> 20 m), the trial carried out in Italy (Colli Euganei area) in 2019 where traps were placed at 5–7 m above the ground and the trappings carried out in some forests of north-central France during 2019–2021 where traps were placed in the upper canopy (> 20 m). Each trap was separated from the next by 50 m at least and traps were preferentially placed at the forest edge. In ports-of-entry, the traps were attached to branches of available trees, at least 2 m above ground with a minimum distance between traps of 100 m. A similar design was used for the traps placed within the 1 km-radius from the ports-of-entry. Duration of trap deployments were variable amongst sites and years, but in the Northern Hemisphere, experiments were mostly conducted from mid-April at the earliest to mid-October at the latest, except in 2020 when the COVID-19 pandemic delayed the onset of trapping until mid-June or mid-July. In Australia, traps were deployed from December to March, depending on the year. Detailed trap heights and trapping duration by site are provided in the Suppl. material 1.

All lures were prepared by INRAE before being shipped to all study participants. These lures consisted of a blend designed by Fan et al. (2019), which contains eight cerambycid pheromones (fuscumol, fuscumol acetate, monochamol, 3-hydroxyhexan-2-one, *anti*-2,3-hexanediol and 2-methylbutan-1-ol, all at 50 mg/ml; geranylacetone- 25 mg/ml; and prionic acid- 0.5 mg/ml; Table 2) dissolved in isopropanol as a carrier to a total volume of 1 ml per lure. The blend composition was expected to attract a large number of cerambycid subfamilies and tribes according to Hanks et al. (2012), (Table 2). Dispensers consisted of a cotton dental pad (to serve as a reservoir and stabilise release rate) placed into a polyethylene sachet (Minigrip, 4 cm × 6 cm × 60 μ; Dutscher, Brumath, France) and dosed with 1 ml of the lure solution. The release rate was estimated by Fan et al. (2019) as 0.0263 ± 0.002 g/d under 20 °C conditions. A dispenser was hung in the centre of each trap.

All primary compounds were obtained from ChemTica Internacional, except prionic acid, which was purchased from Alpha Scents Inc. Commercial high release rate ethanol (100 ml dose, 96% purity, release rate 2 g/day at 20 °C; Econex, Spain) and α-pinene lures (25 ml dose, 98% purity, release rate 0.3 g/day at 20 °C; Econex, Spain) were added to traps in most trials (1076 of the 1308 traps; Table 1). These compounds are known to synergise attraction of some cerambycid species to their pheromones (e.g. Allison et al. 2012; Ryall et al. 2015; Collignon et al. 2016; Miller et al. 2017), but are mildly repellent for others (Collignon et al. 2016). Trap catches were tabulated every 3–4 wk, at which time the pheromone lures were replaced. The ethanol UHR and α-pinene lures, when added, were replaced every 6 wk.

Table 1. Summary of the trapping design per country from 2018 to 2021. Research project: C: CANOPEE; H: HOMED; M: MULTITRAP; P: PORTRAP; S: SAMFIX. Blend: #8: 8-pheromone blend; #8+ET: 8-pheromone blend + ethanol UHR; #8+AP+ ET: 8-pheromone blend + α-pinene + ethanol UHR; #10+ AP+ET: 10- pheromone blend + α-pinene + ethanol UHR. Trap type: MF: multifunnel; CV: crossvane. Trap colour: B: black; G: Green; BG: Black base and green top; P: Purple; Y: Fluorescent yellow; others: brown, blue, red, grey (corresponding to data collected by Cavaletto et al. 2021). Collection type: W: wet; D: dry. Note that the sites could be similar in a country from one year to the next.

Region	Year	Country/ Province	Project	No Sites	No Traps	Blend				Trap type		Trap color						Collection Type	
						#8	#8+ET	#8+AP+ET	#10+AP+ET	MF	CV	B	G	BG	P	Y	Other	W	D
Europe	2018	Austria	M	3	20	10	0	10	0	10	10	20	0	0	0	0	0	0	20
Europe	2018	England	M	3	8	4	0	4	0	6	2	8	0	0	0	0	0	0	8
Europe	2018	France	M,P	32	97	18	0	79	0	41	56	78	7	7	3	0	0	0	97
Europe	2018	Netherlands	M	3	18	6	0	12	0	9	9	9	0	0	0	0	0	18	0
Europe	2019	Austria	H	2	4	0	0	4	0	4	0	4	0	0	0	0	0	0	4
Europe	2019	Bulgaria	H	2	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Europe	2019	Czech Rep	H	2	32	0	0	32	0	32	0	32	0	0	0	0	0	32	0
Europe	2019	England	H	2	4	2	0	2	0	4	0	4	0	0	0	0	0	0	4
Europe	2019	France	C, H, P, S	26	170	0	0	170	0	164	6	89	59	13	9	0	0	88	82
Europe	2019	Greece	H	2	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Europe	2019	Italy	H, S	19	192	0	128	64	0	64	128	48	48	0	16	16	64	192	0
Europe	2019	Portugal	H	2	32	0	0	32	0	32	0	32	0	0	0	0	0	32	0
Europe	2019	Spain	H	1	2	0	0	2	0	2	0	2	0	0	0	0	0	0	2
Europe	2019	Sweden	H	1	16	0	0	16	0	16	0	16	0	0	0	0	0	16	0
Europe	2019	Switzerland	H	2	64	0	0	64	0	64	0	32	32	0	0	0	0	64	0
Europe	2020	France	C, H, P, S	48	166	2	0	64	100	160	6	77	35	17	17	17	0	18	148
Europe	2020	Greece	H	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1
Europe	2020	Italy	H	2	8	0	0	8	0	8	0	2	4	0	2	0	0	0	8
Europe	2020	Portugal	H	2	8	0	0	8	0	8	0	4	4	0	0	0	0	0	8
Europe	2020	Spain	H	6	22	0	0	22	0	22	0	22	0	0	0	0	0	0	22
Europe	2020	Switzerland	H	2	4	0	0	4	0	4	0	4	0	0	0	0	0	4	0
Europe	2021	France	C, H, P, S	58	165	2	0	58	105	162	3	98	42	0	14	11	0	30	135
Europe	2021	Greece	H	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1
Europe	2021	Italy	H	1	4	0	0	4	0	4	0	0	2	0	2	0	0	0	4
Europe	2021	Portugal	H	2	8	0	0	8	0	8	0	4	4	0	0	0	0	0	8
Europe	2021	Slovenia	H	4	18	0	0	18	0	18	0	18	0	0	0	0	0	0	18
Europe	2021	Spain	H	6	16	0	0	16	0	16	0	12	4	0	0	0	0	0	16
Europe	2021	Switzerland	H	9	19	8	0	11	0	19	0	8	11	0	0	0	0	11	8
Europe	Total			244	1105	52	128	720	205	885	220	631	252	37	63	44	64	505	600
Asia	2019	China/Beijing	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3

Region	Year	Country/ Province	Project	No Sites	No Traps	Blend				Trap type			Trap color					Collection Type	
						#8	#8+ET	#8+AP+ET	#10+AP+ET	MF	CV	B	G	BG	P	Y	Other	W	D
Asia	2019	China/Hebei	H	2	6	0	0	6	0	6	0	6	0	0	0	0	0	0	6
Asia	2019	China/InnerMongolia	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2019	China/Liaoning	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2019	China/Yunnan	H	1	4	0	0	4	0	4	0	4	0	0	0	0	0	0	4
Asia	2019	China/Zhejiang	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2020	China/Hebei	H	4	12	0	0	12	0	12	0	12	0	0	0	0	0	0	12
Asia	2020	China/Hunan	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2020	China/Inner Mongolia	H	2	6	0	0	6	0	6	0	6	0	0	0	0	0	0	6
Asia	2020	China/Jiangxi	H	2	6	0	0	6	0	6	0	6	0	0	0	0	0	0	6
Asia	2020	China/Liaoning	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2020	China/Shandong	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2020	China/Yunnan	H	1	4	0	0	4	0	4	0	4	0	0	0	0	0	0	4
Asia	2020	China/Zhejiang	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Beijing	H	1	3	0	0	0	3	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Gansu	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Hebei	H	2	6	0	0	6	0	6	0	6	0	0	0	0	0	0	6
Asia	2021	China/Hunan	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Inner Mongolia	H	2	6	0	0	3	3	6	0	6	0	0	0	0	0	0	6
Asia	2021	China/Jiangxi	H	2	6	0	0	6	0	6	0	6	0	0	0	0	0	0	6
Asia	2021	China/Lioaning	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Shandong	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	China/Yunnan	H	3	5	0	0	0	5	5	0	5	0	0	0	0	0	0	5
Asia	2021	China/Zhejiang	H	1	3	0	0	3	0	3	0	3	0	0	0	0	0	0	3
Asia	2021	Russia/Siberia	H	3	3	3	0	0	0	3	0	3	0	0	0	0	0	0	3
Asia	Total			38	106	3	0	92	11	106	0	106	0	0	0	0	0	0	106
North America	2019	USA/ Michigan	H	9	18	18	0	0	0	18	0	18	0	0	0	0	0	18	0
North America	2019	USA/ Ohio	H	1	32	0	0	32	0	32	0	16	16	0	0	0	0	32	0
North America	2019	Canada/ Nova Scotia	H	1	32	0	0	32	0	32	0	16	16	0	0	0	0	32	0
North America	Total			11	82	18	0	64	0	82	0	50	32	0	0	0	0	82	0
The Caribbean	2020	France/ Martinique	H	2	3	3	0	0	0	3	0	3	0	0	0	0	0	0	3
The Caribbean	2021	France/ Martinique	H	3	4	4	0	0	0	4	0	4	0	0	0	0	0	0	4
The Caribbean	Total			5	7	7	0	0	0	7	0	7	0	0	0	0	0	0	7
Australia	2020	Australia	H	2	4	0	0	4	0	4	0	4	0	0	0	0	0	0	4
Australia	2021	Australia	H	2	4	0	0	4	0	4	0	4	0	0	0	0	0	0	4
Australia	Total			4	8	0	0	8	0	8	0	8	0	0	0	0	0	0	8
Grand total				302	1308	80	0 128	884	216	1088	220	802	284	37	63	44	64	587	721

Table 2. Composition of the 8-pheromone and 10-pheromone blends and targeted sex and cerambycid tribes.

Blend	Compound	Amount/lure (mg/ml)	Target Sex	Target subfamily				Target tribe/ genus	References
				Cerambycinae	Lamiinae	Aseminae	Prioninae		
8-pheromones	Racemic 3-hydroxyhexan-2-one (C6-ketol)	50	M/F	X				Callidiini	Millar et al. (2018)
				X				Clytini	Hanks and Millar (2013), Wickham et al. (2014), Bobadoye et al. (2019)
				X				Hesperophanini	unpub data JGM
				X				Hylotrupini	Reddy et al. (2005)
8-pheromones	Racemic 2-methylbutan-1-ol	50	M/F	X				Callidiini	Hanks et al. (2018)
8-pheromones	2*R**,3*S**-2,3-hexanediol	50	M/F	X				Clytini	Hanks and Millar (2013), Wickham et al. (2014)
8-pheromones	Racemic fuscumol + fuscumol acetate	50+ 50	M/F	X				Obriini	Millar et al. (2018)
					X			Acanthocinini	Millar et al. (2018)
					X			Acanthoderini	Hanks and Millar (2013)
						X		Asemini	Millar et al. (2018)
8-pheromones	Monochamol	50	M/F		X			Monochamini	Hanks et al. (2018)
					X			Lamiini	Wickham et al. (2014)
8-pheromones	Geranylacetone	25	M/F		X			Acanthocinini	Meier et al. (2016, 2019)
						X		Asemini	Halloran et al. (2018)
8-pheromones	Prionic acid (4 stereoisomers)	05	M				X	Prionini	Barbour et al. (2011)
10-pheromones	Racemic trichoferone	25	M/F	X				*Trichoferus*	Ray et al. (2019)
10-pheromones	(*E*)-2-*cis*-6,7-epoxynonenal	50	M/F	X				*Aromia*	Xu et al. (2017)

In most cases, the trapped insects were killed using a section of mesh impregnated with α-cypermethrin insecticide (Storanet, BASF Pflanzenschutz Deutschland, Germany) placed into the trap basins, whose bottoms had been replaced with a wire mesh to allow drainage and to keep specimens dry. However, in the targeted 2019 experiment in forests near ports-of-entry and in the Colli Euganei area (Italy), "wet" trap basins were used, containing water-diluted propylene glycol (50%) to act as a surfactant and preservative. In the trials conducted in Ohio and Michigan, trap collection cups were filled with ~ 200–400 ml of undiluted propylene glycol.

Trapped cerambycids were identified to species by local specialists or sent to INRAE for identification. However, specimens trapped in Australia could not be sent due to restrictions by the customs agency and so most could only be identified to the genus level. Nomenclature used in this article follows the reference checklist of the world database Titan (Tavakilian and Chevillotte 2022).

Preliminary tests of a 10-pheromone blend

In 2020 and 2021, two additional pheromones, trichoferone (the pheromone of *T. campestris*) and (*E*)-2-*cis*-6,7-epoxynonenal (the pheromone of *A. bungii*), were added to the 8-pheromone lures used in France and China, to test for a possible increase in

monitoring effectiveness with a 10-pheromone blend (Table 2). Both compounds were synthesised by YFZ and JGM at the University of California, Riverside, using previously-reported syntheses (Ray et al. 2019; Xu et al. 2017, respectively). Lure preparation and insect collection procedures were similar to those described above. Captures were compared with those of the 8-pheromone blend at six sites in France during 2020 by deploying five pairs of traps baited with each blend at each site. The traps were spaced ~ 100 m apart and rotated at each insect collection, which enabled the number of collection dates at each site to be used as replicates. The Student *t*-test for paired samples was then applied to compare the number of species trapped by each lure.

Results

A total of 78,321 longhorned beetles were trapped, representing 376 species, including 373 Cerambycidae, two Vesperidae and one Disteniidae species (Table 3). The cerambycids belonged to eight subfamilies, including 156 species of Cerambycinae, 102 species of Lamiinae, 78 species of Lepturinae, 21 species of Spondylidinae, 12 species of Prioninae, two species of Necydalinae and one species of Parandrinae (Fig. 1). Captures comprised 60 tribes, with 10 tribes including more than nine species trapped on different continents; in decreasing order the tribe Clytini (64 spp.), followed by Lepturini (44 spp.), Rhagiini (32 spp.), Acanthocinini (31 spp.), Callidiini (20 spp.), Monochamini (18 spp.), Saperdini (10 spp.) and Aseminii, Pogonocherini and Prionini (nine spp.

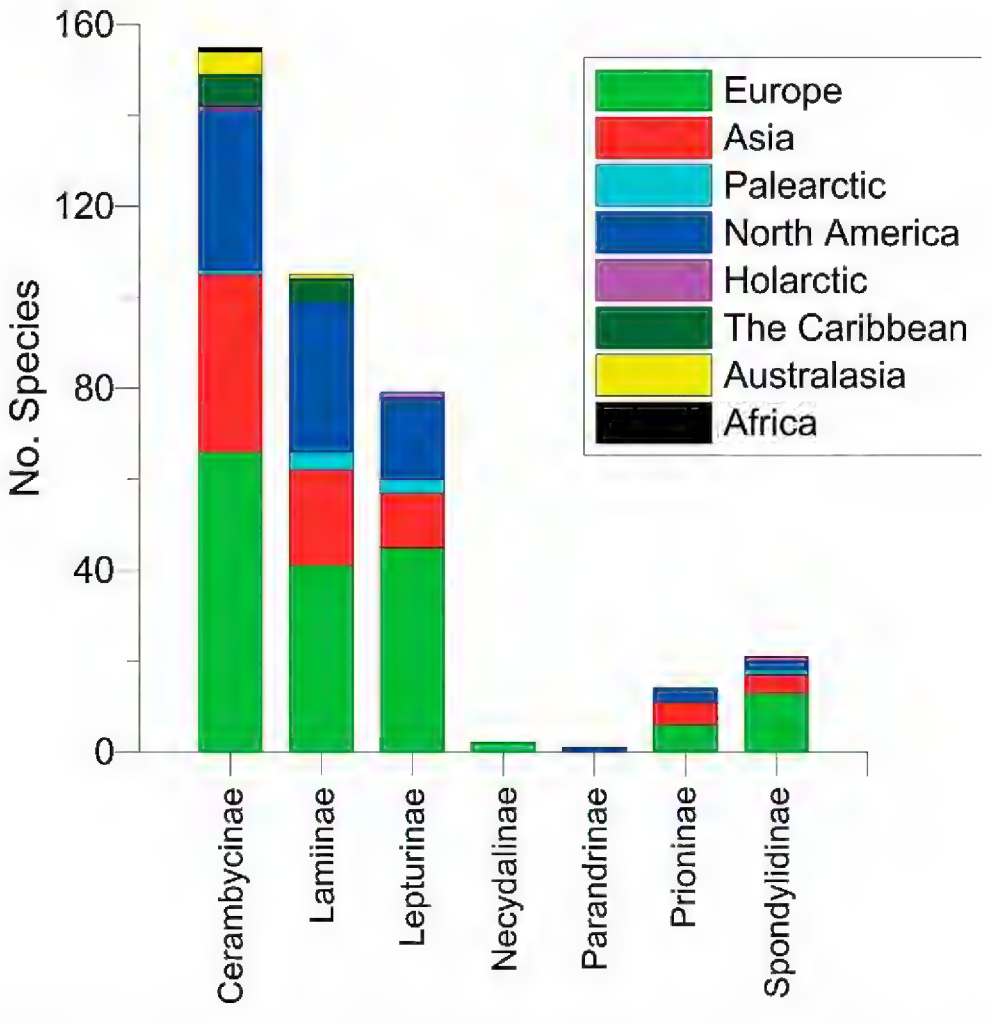

Figure 1. Number of species trapped per subfamily and their region of origin.

each; Fig. 2). Generally, fewer species were trapped in the Caribbean and Australia, where only a limited number of traps had been deployed. Some of the captured species belonged to tribes other than those targeted, such as Callidiopini (*Curtomerus flavus* [F.] in Martinique and *Bethelium* sp. in Australia), Eburiini (*Eburia* spp. in Martinique) and Tillomorphini (*Gourbeyrella madininae* Chalumeau & Touroult in Martinique).

Most tribes included species from the same genera trapped on different continents (Fig. 2). For example, 19 species of the Clytini genus *Xylotrechus* were captured, including 10 in Asia, five in Europe and four in North America. In the same tribe, 12 species of *Chlorophorus* were captured, of which eight were caught in Europe and four in Asia. A total of 12 *Monochamus* species (Lamiinae, Monochamini) were trapped, including five species in Asia, four in North America and three in Europe. The Callidiini genus *Phymatodes* was represented by 11 species, including seven in Europe and four in North America. A number of these species had not been trapped before by any semiochemically-baited trap (e.g. *X. chinensis*, *Chlorophorus glabromaculatus* [Goeze] and *Phymatodes pusillus* [F.]).

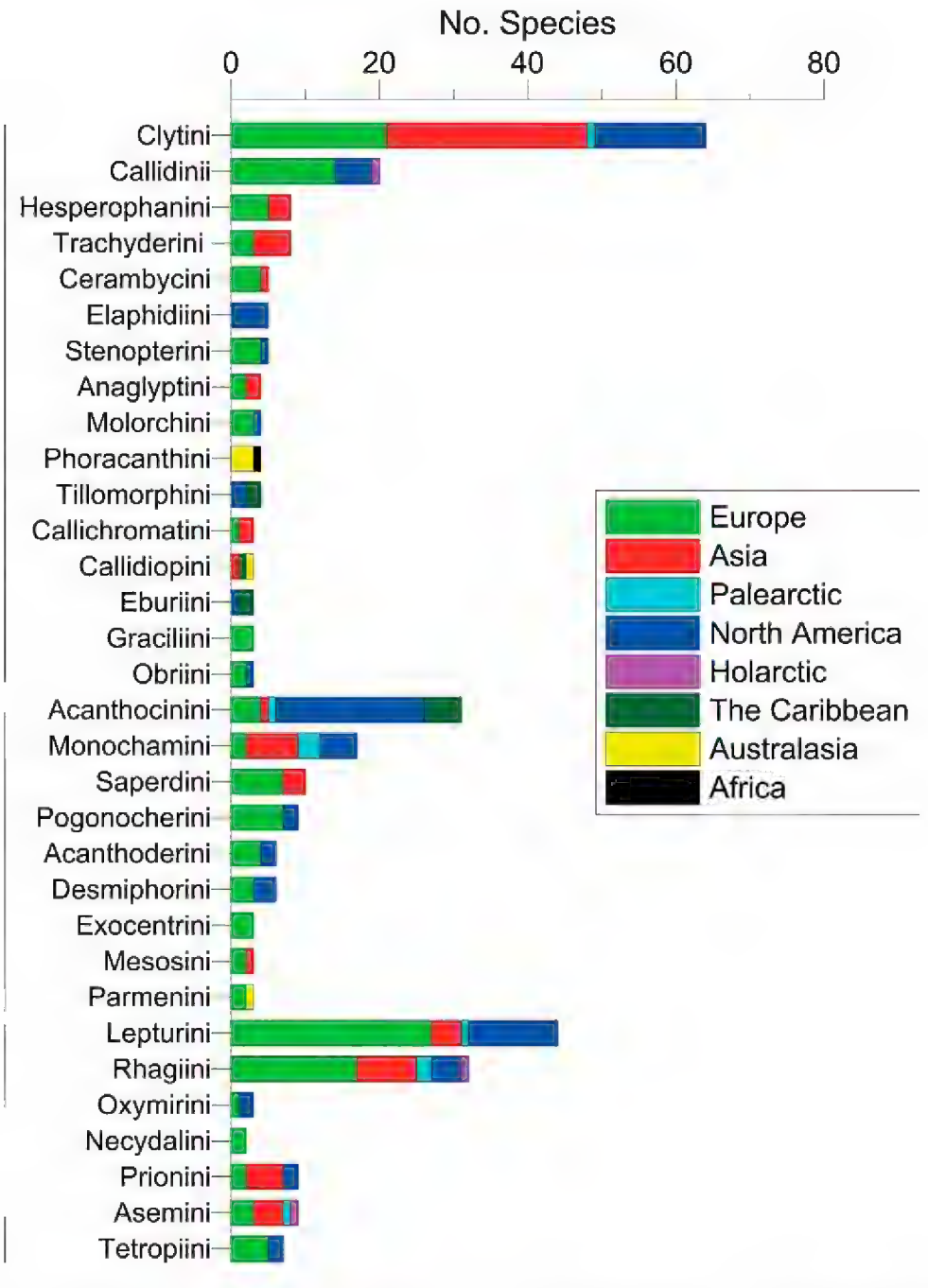

Figure 2. Number of species trapped per tribe in decreasing order and their native region. Only the tribes where > 3 spp were captured are shown.

Table 3. Names of trapped species, origin and specimen numbers captured per continent. Species in bold were trapped in non-native continents.

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Cerambycinae	Anaglyptini	*Anaglyptus gibbosus* (Fabricius, 1787)	Europe	105	0	0	0	0	105
Cerambycinae	Anaglyptini	*Anaglyptus mysticus* (Linnaeus, 1758)	Europe	116	0	0	0	0	116
Cerambycinae	Anaglyptini	*Cyrtophorus verrucosus* (Olivier, 1800)	North America	0	0	197	0	0	197
Cerambycinae	Anaglyptini	*Microclytus compressicollis* (Laporte de Castelnau & Gory, 1841)	North America	0	0	2	0	0	2
Cerambycinae	Bothriospilini	*Chlorida festiva* (Linnaeus, 1758)	Caribbean	0	0	0	0	2	2
Cerambycinae	Callichromatini	*Aromia bungii* Faldermann, 1835	Asia	0	25	0	0	0	25
Cerambycinae	Callichromatini	*Aromia moschata* (Linnaeus, 1758)	Europe	30	0	0	0	0	30
Cerambycinae	Callichromatini	*Aromia moschata orientalis* Plavilstshikov, 1933	Asia	0	3	0	0	0	3
Cerambycinae	Callidiini	*Callidium aeneum* (Degeer, 1775)	Holarctic	120	79	0	0	0	199
Cerambycinae	Callidiini	*Callidium violaceum* (Linnaeus, 1758)	Europe	3	0	0	0	0	3
Cerambycinae	Callidiini	*Lioderina linearis* (Hampe, 1870)	Europe	3	0	0	0	0	3
Cerambycinae	Callidiini	*Phymatodes aereus* (Newman, 1838)	North America	0	0	14	0	0	14
Cerambycinae	Callidiini	*Phymatodes alni* (Linnaeus, 1767)	Europe	2295	0	0	0	0	2295
Cerambycinae	Callidiini	*Phymatodes amoenus* (Say, 1824)	North America	0	0	3100	0	0	3100
Cerambycinae	Callidiini	*Phymatodes dimidiatus* (Kirby, 1837)	North America	0	0	55	0	0	55
Cerambycinae	Callidiini	*Phymatodes fasciatus* (Villers, 1789)	Europe	6	0	0	0	0	6
Cerambycinae	Callidiini	*Phymatodes glabratus* (Charpentier, 1825)	Europe	3	0	0	0	0	3
Cerambycinae	Callidiini	*Phymatodes lividus* (Rossi, 1794)	Europe	7	0	0	0	0	7
Cerambycinae	Callidiini	*Phymatodes pusillus* (Fabricius, 1787)	Europe	37	0	0	0	0	37
Cerambycinae	Callidiini	*Phymatodes rufipes* (Fabricius, 1776)	Europe	3	0	0	0	0	3
Cerambycinae	Callidiini	***Phymatodes testaceus* (Linnaeus, 1758)**	Europe	15085	0	41	0	0	15126
Cerambycinae	Callidiini	*Phymatodes varius* (Fabricius, 1776)	North America	0	0	29	0	0	29
Cerambycinae	Callidiini	*Physocnemum brevilineum* (Say, 1824)	North America	0	0	4	0	0	4
Cerambycinae	Callidiini	*Pyrrhidium sanguineum* (Linnaeus, 1758)	Europe	4388	0	0	0	0	4388
Cerambycinae	Callidiini	*Ropalopus clavipes* (Fabricius, 1775)	Europe	69	0	0	0	0	69
Cerambycinae	Callidiini	*Ropalopus femoratus* (Linnaeus, 1758)	Europe	35	0	0	0	0	35
Cerambycinae	Callidiini	*Ropalopus macropus* (Germar, 1823)	Europe	21	0	0	0	0	21
Cerambycinae	Callidiini	*Ropalopus varini* (Bedel, 1870)	Europe	1	0	0	0	0	1
Cerambycinae	Callidiopini	*Bethelium* sp.	Australasia	0	0	0	5	0	5
Cerambycinae	Callidiopini	*Curtomerus flavus* (Fabricius, 1775)	Caribbean	0	0	0	0	7	7
Cerambycinae	Callidiopini	*Stenodryas clavigera* Bates, 1873	Asia	0	1	0	0	0	1
Cerambycinae	Cerambycini	*Cerambyx cerdo* Linnaeus, 1758	Europe	20	0	0	0	0	20
Cerambycinae	Cerambycini	*Cerambyx miles* Bonelli, 1812	Europe	3	0	0	0	0	3
Cerambycinae	Cerambycini	*Cerambyx scopolii* Fueßlins, 1775	Europe	141	0	0	0	0	141
Cerambycinae	Cerambycini	*Cerambyx welensii* (Küster, 1845)	Europe	22	0	0	0	0	22
Cerambycinae	Cerambycini	*Nadezhdiella cantori* (Hope, 1842)	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Chlorophorus figuratus* (Scopoli, 1763)	Europe	42	0	0	0	0	42
Cerambycinae	Clytini	*Chlorophorus glabromaculatus* (Goeze, 1777)	Europe	1391	0	0	0	0	1391
Cerambycinae	Clytini	*Chlorophorus glaucus* (Fabricius, 1781)	Europe	36	0	0	0	0	36
Cerambycinae	Clytini	*Chlorophorus herbstii* (Brahm, 1790)	Europe	6	0	0	0	0	6
Cerambycinae	Clytini	*Chlorophorus miwai* Gressitt, 1936	Asia	0	9	0	0	0	9
Cerambycinae	Clytini	*Chlorophorus motschulskyi* (Ganglbauer, 1887)	Asia	0	7	0	0	0	7
Cerambycinae	Clytini	*Chlorophorus ruficornis* (Olivier, 1790)	Europe	41	0	0	0	0	41
Cerambycinae	Clytini	*Chlorophorus sartor* (Müller, 1766)	Europe	482	0	0	0	0	482
Cerambycinae	Clytini	*Chlorophorus signaticollis* (Laporte de Castelnau & Gory, 1836)	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Chlorophorus tredecimmaculatus* (Chevrolat, 1863)	Asia	0	2	0	0	0	2
Cerambycinae	Clytini	*Chlorophorus trifasciatus* (Fabricius, 1781)	Europe	33	0	0	0	0	33

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Cerambycinae	Clytini	*Chlorophorus varius* (Müller, 1766)	Europe	36	0	0	0	0	36
Cerambycinae	Clytini	*Clytoleptus albofasciatus* (Laporte de Castelnau & Gory, 1841)	North America	0	0	6	0	0	6
Cerambycinae	Clytini	*Clytus arietis* (Linnaeus, 1758)	Europe	52	0	0	0	0	52
Cerambycinae	Clytini	*Clytus lama* Mulsant, 1850	Europe	123	0	0	0	0	123
Cerambycinae	Clytini	*Clytus rhamni* Germar, 1817	Europe	85	0	0	0	0	85
Cerambycinae	Clytini	*Clytus ruricola* (Olivier, 1800)	North America	0	0	25	0	0	25
Cerambycinae	Clytini	*Clytus tropicus* (Panzer, 1795)	Europe	73	0	0	0	0	73
Cerambycinae	Clytini	*Cyrtoclytus capra* (Germar, 1823)	Asia	0	24	0	0	0	24
Cerambycinae	Clytini	*Cyrtoclytus caproides* (Bates, 1873)	Asia	0	5	0	0	0	5
Cerambycinae	Clytini	*Demonax diversefasciatus* Pic, 1920	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Demonax nansenensis* Pic 1903	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Demonax sp. 1*	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Demonax sp. 2*	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Glycobius speciosus* (Say, 1824)	North America	0	0	1	0	0	1
Cerambycinae	Clytini	*Isotomus speciosus* (Schneider, 1787)	Europe	1	0	0	0	0	1
Cerambycinae	Clytini	*Megacyllene caryae* (Gahan, 1908)	North America	0	0	22	0	0	22
Cerambycinae	Clytini	***Neoclytus acuminatus acuminatus* (Fabricius, 1775)**	North America	37	0	28	0	0	65
Cerambycinae	Clytini	*Neoclytus caprea* (Say, 1824)	North America	0	0	3	0	0	3
Cerambycinae	Clytini	*Neoclytus leucozonus* (Laporte de Castelnau & Gory, 1841)	North America	0	0	15	0	0	15
Cerambycinae	Clytini	*Neoclytus mucronatus mucronatus* (Fabricius, 1775)	North America	0	0	323	0	0	323
Cerambycinae	Clytini	*Neoclytus muricatulus* (Kirby, 1837)	North America	0	0	1	0	0	1
Cerambycinae	Clytini	*Neoclytus scutellaris* (Olivier, 1790)	North America	0	0	2	0	0	2
Cerambycinae	Clytini	*Perissus paulonotatus* (Pic, 1902)	Asia	0	21	0	0	0	21
Cerambycinae	Clytini	*Plagionotus arcuatus* (Linnaeus, 1758)	Europe	95	0	0	0	0	95
Cerambycinae	Clytini	*Plagionotus christophi* (Kraatz, 1879)	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Plagionotus detritus* (Linnaeus, 1758)	Europe	299	0	0	0	0	299
Cerambycinae	Clytini	*Pseudosphegesthes cinerea* (Laporte de Castelnau & Gory, 1841)	Europe	27	0	0	0	0	27
Cerambycinae	Clytini	*Raphuma anongi* Gressitt & Rondon, 1970	Asia	0	96	0	0	0	96
Cerambycinae	Clytini	*Raphuma gracilipes* (Faldermann, 1835)	Asia	0	24	0	0	0	24
Cerambycinae	Clytini	*Raphuma laosica* Gressitt & Rondon, 1970	Asia	0	22	0	0	0	22
Cerambycinae	Clytini	*Raphuma* sp.	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Rhabdoclytus acutivittis* (Kraatz, 1879)	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Sarosesthes fulminans* (Fabricius, 1775)	North America	0	0	39	0	0	39
Cerambycinae	Clytini	*Xylotrechus antilope* (Schönherr, 1817)	Europe	1303	0	0	0	0	1303
Cerambycinae	Clytini	*Xylotrechus antilope* var *sekerai* Podaný, 1970	Europe	16	0	0	0	0	16
Cerambycinae	Clytini	*Xylotrechus arvicola* (Olivier, 1800)	Europe	379	0	0	0	0	379
Cerambycinae	Clytini	*Xylotrechus atronotatus* Pic, 1917	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus buqueti* (Laporte de Castelnau & Gory, 1841)	Asia	0	38	0	0	0	38
Cerambycinae	Clytini	***Xylotrechus chinensis* (Chevrolat, 1852)**	Asia	41	3	0	0	0	44
Cerambycinae	Clytini	*Xylotrechus clarinus* Bates, 1884	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus colonus* (Fabricius, 1775)	North America	0	0	484	0	0	484
Cerambycinae	Clytini	*Xylotrechus gratus* Viktora, 2020	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus integer* (Haldeman, 1847)	North America	0	0	1	0	0	1
Cerambycinae	Clytini	*Xylotrechus latefasciatus ochroceps* Gressitt, 1951	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus magnicollis* (Fairmaire, 1888)	Asia	0	1	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus pantherinus* (Savenius, 1825)	Europe	1	0	0	0	0	1
Cerambycinae	Clytini	*Xylotrechus pekingensis* Pic, 1939	Asia	0	1	0	0	0	1

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Cerambycinae	Clytini	*Xylotrechus rufilius* Bates, 1884	Asia	0	27	0	0	0	27
Cerambycinae	Clytini	*Xylotrechus rusticus* (Linnaeus, 1758)	Europe/Asia	161	1	0	0	0	162
Cerambycinae	Clytini	*Xylotrechus sagittatus* (Germar, 1821)	North America	0	0	34	0	0	34
Cerambycinae	Clytini	***Xylotrechus stebbingi* Gahan, 1906**	Asia	6089	0	0	0	0	6054
Cerambycinae	Clytini	*Xylotrechus undulatus* (Say, 1824)	North America	0	0	26	0	0	26
Cerambycinae	Deilini	*Deilus fugax* (Olivier, 1790)	Europe	87	0	0	0	0	87
Cerambycinae	Dryobiini	*Dryobius sexnotatus* Linsley, 1957	North America	0	0	2	0	0	2
Cerambycinae	Eburiini	*Eburia dejeani* Gahan, 1895	Caribbean	0	0	0	0	2	2
Cerambycinae	Eburiini	*Eburia octomaculata* Chevrolat, 1862	Caribbean	0	0	0	0	1	1
Cerambycinae	Eburiini	*Eburia quadrigeminata* (Say, 1827)	North America	0	0	3	0	0	3
Cerambycinae	Elaphidiini	*Anelaphus pumilus* (Newman, 1840)	North America	0	0	531	0	0	531
Cerambycinae	Elaphidiini	*Anelaphus villosus* (Fabricius, 1793)	North America	0	0	8	0	0	8
Cerambycinae	Elaphidiini	*Elaphidion mucronatum* (Say, 1824)	North America	0	0	110	0	0	110
Cerambycinae	Elaphidiini	*Parelaphidion aspersum* (Haldeman, 1847)	North America	0	0	3	0	0	3
Cerambycinae	Elaphidiini	*Parelaphidion incertum* (Newman, 1840)	North America	0	0	4	0	0	4
Cerambycinae	Graciliini	*Axinopalpis gracilis* (Krynicki, 1832)	Europe	8	0	0	0	0	8
Cerambycinae	Graciliini	*Gracilia minuta* (Fabricius, 1781)	Europe	12	0	0	0	0	12
Cerambycinae	Graciliini	*Penichroa fasciata* (Stephens, 1831)	Europe	41	0	0	0	0	41
Cerambycinae	Hesperophanini	*Gnatholea eburifera* Thomson, 1861	Asia	0	10	0	0	0	10
Cerambycinae	Hesperophanini	*Hesperophanes sericeus* (Fabricius, 1787)	Europe	8	0	0	0	0	8
Cerambycinae	Hesperophanini	*Stromatium auratum* (Böber, 1793)	Europe	7	0	0	0	0	7
Cerambycinae	Hesperophanini	***Trichoferus campestris* (Faldermann, 1835)**	Asia	45	12	0	0	0	57
Cerambycinae	Hesperophanini	*Trichoferus fasciculatus* (Faldermann, 1837)	Europe	135	0	0	0	0	135
Cerambycinae	Hesperophanini	*Trichoferus guerryi* (Pic, 1915)	Asia	0	1	0	0	0	1
Cerambycinae	Hesperophanini	*Trichoferus holosericeus* (Rossi, 1790)	Europe	187	0	0	0	0	187
Cerambycinae	Hesperophanini	*Trichoferus pallidus* (Olivier, 1790)	Europe	145	0	0	0	0	145
Cerambycinae	Hylotrupini	*Hylotrupes bajulus* (Linnaeus, 1758)	Europe	79	0	0	0	0	79
Cerambycinae	Molorchini	*Dolocerus reichii* Mulsant, 1862	Europe	1	0	0	0	0	1
Cerambycinae	Molorchini	*Molorchus bimaculatus* Say, 1824	North America	0	0	122	0	0	122
Cerambycinae	Molorchini	*Molorchus minor* (Linnaeus, 1758)	Europe	15	0	0	0	0	15
Cerambycinae	Molorchini	*Molorchus umbellatarum* (Schreber, 1759)	Europe	55	0	0	0	0	55
Cerambycinae	Neoibidionini	*Neocompsa cylindricollis* (Fabricius, 1798)	Caribbean	0	0	0	0	1	1
Cerambycinae	Obriini	*Obrium brunneum* (Fabricius, 1793)	Europe	3	0	0	0	0	3
Cerambycinae	Obriini	*Obrium cantharinum* (Linnaeus, 1767)	Europe	44	0	0	0	0	44
Cerambycinae	Obriini	*Obrium maculatum* (Olivier, 1800)	North America	0	0	1	0	0	1
Cerambycinae	Phoracanthini	***Cordylomera spinicornis* (Fabricius, 1775)**	Africa	4	0	0	0	0	4
Cerambycinae	Phoracanthini	***Phoracantha recurva* Newman, 1840**	Australasia	8	0	0	0	0	8
Cerambycinae	Phoracanthini	***Phoracantha semipunctata* (Fabricius, 1775)**	Australasia	11	0	0	0	0	11
Cerambycinae	Phoracanthini	*Thoris* sp.	Australasia	0	0	0	2	0	2
Cerambycinae	Psebiini	*Nathrius brevipennis* (Mulsant, 1839)	Europe	649	0	0	0	0	649
Cerambycinae	Pytheini	*Certallum ebulinum* (Linnaeus, 1767)	Europe	1	0	0	0	0	1
Cerambycinae	Rhopalophorini	*Rhopalophora longipes* (Say, 1824)	North America	0	0	1	0	0	1
Cerambycinae	Stenhomalini	*Stenhomalus fenestratus* White,1855	Asia	0	3	0	0	0	3
Cerambycinae	Stenoderini	*Syllitus* sp.	Australasia	0	0	0	2	0	2
Cerambycinae	Stenopterini	*Callimoxys sanguinicollis* (Olivier, 1800)	North America	0	0	1	0	0	1
Cerambycinae	Stenopterini	*Callimus abdominalis* (Olivier, 1800)	Europe	11	0	0	0	0	11
Cerambycinae	Stenopterini	*Callimus angulatus* (Schrank, 1789)	Europe	1	0	0	0	0	1
Cerambycinae	Stenopterini	*Stenopterus ater* (Linnaeus, 1767)	Europe	20	0	0	0	0	20
Cerambycinae	Stenopterini	*Stenopterus rufus* (Linnaeus, 1767)	Europe	83	0	0	0	0	83
Cerambycinae	Tillomorphini	*Bonfilsia pejoti* Chalumeau & Touroult, 2004	Caribbean	0	0	0	0	1	1

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Cerambycinae	Tillomorphini	*Euderces picipes* (Fabricius, 1787)	North America	0	0	9	0	0	9
Cerambycinae	Tillomorphini	*Euderces pini* (Olivier, 1800)	North America	0	0	93	0	0	93
Cerambycinae	Tillomorphini	*Gourbeyrella madininae* Chalumeau & Touroult, 2004	Caribbean	0	0	0	0	3	3
Cerambycinae	Trachyderini	*Anoplistes halodendri* (Pallas, 1773)	Asia	0	2	0	0	0	2
Cerambycinae	Trachyderini	*Dicelosternus corallinus* Gahan, 1900	Asia	0	3	0	0	0	3
Cerambycinae	Trachyderini	*Purpuricenus budensis* (Götz, 1783)	Europe	18	0	0	0	0	18
Cerambycinae	Trachyderini	*Purpuricenus globulicollis* Dejean, 1839	Europe	2	0	0	0	0	2
Cerambycinae	Trachyderini	*Purpuricenus kaehleri* (Linnaeus, 1758)	Europe	261	0	0	0	0	261
Cerambycinae	Trachyderini	*Purpuricenus lituratus* Ganglbauer, 1887	Asia	0	1	0	0	0	1
Cerambycinae	Trachyderini	*Purpuricenus temminckii* (Guérin-Méneville, 1844)	Asia	0	10	0	0	0	10
Cerambycinae	Trachyderini	*Amarysius altajensis* (Laxmann, 1770)	Asia	0	20	0	0	0	20
Lamiinae	Acanthocinini	*Acanthocinus aedilis* (Linnaeus, 1758)	Europe/Asia	6	24	0	0	0	30
Lamiinae	Acanthocinini	*Acanthocinus griseus* (Fabricius, 1793)	Europe/Asia	114	106	0	0	0	220
Lamiinae	Acanthocinini	*Acanthocinus pusillus* (Kirby, 1837)	North America	0	0	21	0	0	21
Lamiinae	Acanthocinini	*Amniscus similis* (Gahan, 1895)	Caribbean	0	0	0	0	5	5
Lamiinae	Acanthocinini	*Astyleiopus variegatus* (Haldeman, 1847)	North America	0	0	11	0	0	11
Lamiinae	Acanthocinini	*Astylidius parvus* (LeConte, 1873)	North America	0	0	17	0	0	17
Lamiinae	Acanthocinini	*Astylopsis macula* (Say, 1827)	North America	0	0	47	0	0	47
Lamiinae	Acanthocinini	*Astylopsis sexguttata* (Say, 1827)	North America	0	0	19	0	0	19
Lamiinae	Acanthocinini	*Astylopsis* sp.	North America	0	0	2	0	0	2
Lamiinae	Acanthocinini	*Graphisurus despectus* (LeConte, 1850)	North America	0	0	3	0	0	3
Lamiinae	Acanthocinini	*Graphisurus fasciatus* (Degeer, 1775)	North America	0	0	86	0	0	86
Lamiinae	Acanthocinini	*Graphisurus triangulifer* (Haldeman, 1847)	North America	0	0	3	0	0	3
Lamiinae	Acanthocinini	*Hyperplatys maculatus* Haldeman, 1847	North America	0	0	4	0	0	4
Lamiinae	Acanthocinini	*Lagocheirus araneiformis insulorum* Dillon, 1957	Caribbean	0	0	0	0	4	4
Lamiinae	Acanthocinini	*Leiopus fallaciosus* Holzschuh, 1993	Asia	0	5	0	0	0	5
Lamiinae	Acanthocinini	*Leiopus femoratus* Fairmaire, 1859	Europe	3461	0	0	0	0	3461
Lamiinae	Acanthocinini	*Leiopus linnei* Wallin, Nylander & Kvamme, 2009	Europe	548	0	0	0	0	548
Lamiinae	Acanthocinini	*Leiopus nebulosus* (Linneus, 1758)	Europe	1473	0	0	0	0	1473
Lamiinae	Acanthocinini	*Leptostylus transversus* (Gyllenhal, 1817)	North America	0	0	101	0	0	101
Lamiinae	Acanthocinini	*Lepturges angulatus* (LeConte, 1852)	North America	0	0	20	0	0	20
Lamiinae	Acanthocinini	*Lepturges confluens* (Haldeman, 1847)	North America	0	0	26	0	0	26
Lamiinae	Acanthocinini	*Lepturges* sp.	North America	0	0	2	0	0	2
Lamiinae	Acanthocinini	*Sternidius alpha* (Say, 1827)	North America	0	0	3	0	0	3
Lamiinae	Acanthocinini	*Sternidius punctatus* (Haldeman, 1847)	North America	0	0	1	0	0	1
Lamiinae	Acanthocinini	*Sternidius rusticus* (LeConte, 1852)	North America	0	0	19	0	0	19
Lamiinae	Acanthocinini	*Styloleptus posticalis* (Gahan, 1895)	Caribbean	0	0	0	0	1	1
Lamiinae	Acanthocinini	*Trypanidius spilmani* Villiers, 1980	Caribbean	0	0	0	0	1	1
Lamiinae	Acanthocinini	*Urgleptes cobbeni* Gilmour, 1963	Caribbean	0	0	0	0	1	1
Lamiinae	Acanthocinini	*Urgleptes querci* (Fitch, 1859)	North America	0	0	2	0	0	2
Lamiinae	Acanthocinini	*Urgleptes signatus* (LeConte, 1852)	North America	0	0	1	0	0	1
Lamiinae	Acanthoderini	*Aegomorphus clavipes* (Schrank von Paula, 1781)	Europe	1412	0	0	0	0	1412
Lamiinae	Acanthoderini	*Aegomorphus francottei* Sama, 1994	Europe	181	0	0	0	0	181
Lamiinae	Acanthoderini	*Aegomorphus krueperi* (Kraatz, 1859)	Europe	7	0	0	0	0	7
Lamiinae	Acanthoderini	*Aegomorphus modestus* (Blais, 1817)	North America	0	0	58	0	0	58
Lamiinae	Acanthoderini	*Aegomorphus quadrigibbus* (Say, 1831)	North America	0	0	3	0	0	3
Lamiinae	Acanthoderini	*Oplosia cinerea* (Mulsant, 1839)	Europe	63	0	0	0	0	63
Lamiinae	Acanthoderini	*Oplosia nubila* (LeConte, 1862)	North America	0	0	4	0	0	4

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Lamiinae	Agapanthiini	*Agapanthia cardui* (Linnaeus, 1767)	Europe	1	0	0	0	0	1
Lamiinae	Agapanthiini	*Agapanthia villosoviridescens* (Degeer, 1775)	Europe	1	0	0	0	0	1
Lamiinae	Apomecynini	*Apomecyna saltator* (Fabricius, 1787)	Asia	0	1	0	0	0	1
Lamiinae	Ceroplesini	*Moechotypa diphysis* (Pascoe, 1871)	Asia	0	2	0	0	0	2
Lamiinae	Ceroplesini	*Thysia wallichii tonkinensis* (Kreische, 1924)	Asia	0	1	0	0	0	1
Lamiinae	Desmiphorini	*Anaesthetis testacea* (Fabricius, 1781)	Europe	17	0	0	0	0	17
Lamiinae	Desmiphorini	*Deroplia genei* (Aragona, 1830)	Europe	1	0	0	0	0	1
Lamiinae	Desmiphorini	*Deroplia troberti* (Mulsant, 1843)	Europe	3	0	0	0	0	3
Lamiinae	Desmiphorini	*Eupogonius pauper* LeConte, 1852	North America	0	0	1	0	0	1
Lamiinae	Desmiphorini	*Eupogonius tomentosus* (Haldeman, 1847)	North America	0	0	3	0	0	3
Lamiinae	Desmiphorini	*Psenocerus supernotatus* (Say, 1824)	North America	0	0	9	0	0	9
Lamiinae	Dorcaschematini	*Dorcaschema cinereum* (Olivier, 1800)	North America	0	0	1	0	0	1
Lamiinae	Dorcaschematini	*Olenecamptus bilobus* (Fabricius, 1801)	Asia	0	3	0	0	0	3
Lamiinae	Exocentrini	*Exocentrus adspersus* Mulsant, 1846	Europe	5	0	0	0	0	5
Lamiinae	Exocentrini	*Exocentrus lusitanus* (Linnaeus, 1767)	Europe	29	0	0	0	0	29
Lamiinae	Exocentrini	*Exocentrus punctipennis* Mulsant & Guillebeau, 1856	Europe	28	0	0	0	0	28
Lamiinae	Lamiini	*Lamiomimus gottschei* Kolbe, 1886	Asia	0	1	0	0	0	1
Lamiinae	Lamiini	*Pharsalia subgemmata* (Thomson, 1857)	Asia	0	375	0	0	0	375
Lamiinae	Mesosini	*Mesosa curculionoides* (Linnaeus 1761)	Europe	37	0	0	0	0	37
Lamiinae	Mesosini	*Mesosa myops* (Dalman, 1817)	Asia	0	29	0	0	0	29
Lamiinae	Mesosini	*Mesosa nebulosa* (Fabricius, 1781)	Europe	132	0	0	0	0	132
Lamiinae	Monochamini	*Anoplophora beryllina* (Hope, 1840)	Asia	0	1	0	0	0	1
Lamiinae	Monochamini	*Anoplophora chinensis* (Forster, 1771)	Asia	0	1	0	0	0	1
Lamiinae	Monochamini	*Anoplophora glabripennis* (Motschulsky, 1854)	Asia	0	9	0	0	0	9
Lamiinae	Monochamini	*Microgoes oculatus* (LeConte, 1862)	North America	0	0	3	0	0	3
Lamiinae	Monochamini	*Monochamus alternatus* Hope, 1842	Asia	0	1246	0	0	0	1246
Lamiinae	Monochamini	*Monochamus bimaculatus* Gahan, 1888	Asia	0	1	0	0	0	1
Lamiinae	Monochamini	*Monochamus carolinensis* (Olivier, 1797)	North America	0	0	77	0	0	77
Lamiinae	Monochamini	*Monochamus galloprovincialis* (Olivier, 1800)	Europe/Asia	6209	87	0	0	0	6296
Lamiinae	Monochamini	*Monochamus maculosus* Haldeman, 1847	North America	0	0	3	0	0	3
Lamiinae	Monochamini	*Monochamus notatus* (Drury, 1773)	North America	0	0	256	0	0	256
Lamiinae	Monochamini	*Monochamus saltuarius* Gebler, 1830	Asia/Europe	13	985	0	0	0	998
Lamiinae	Monochamini	*Monochamus sartor* (Fabricius, 1787)	Europe	20	0	0	0	0	20
Lamiinae	Monochamini	*Monochamus sartor urussovii* (Fischer von Waldheim, 1806)	Asia/Europe	1	41	0	0	0	42
Lamiinae	Monochamini	*Monochamus scutellatus* (Say, 1824)	North America	0	0	216	0	0	216
Lamiinae	Monochamini	*Monochamus sutor* (Linnaeus, 1758)	Europe/Asia	30	22	0	0	0	52
Lamiinae	Monochamini	*Monochamus sutor longulus* Pic, 1898	Asia	0	22	0	0	0	22
Lamiinae	Monochamini	*Uraecha angusta* (Pascoe, 1857)	Asia	0	15	0	0	0	15
Lamiinae	Obereini	*Oberea linearis* (Linnaeus, 1761)	Europe	8	0	0	0	0	8
Lamiinae	Parmenini	*Mesolita* sp.	Australasia	0	0	0	3	0	3
Lamiinae	Parmenini	*Parmena balteus* (Linnaeus, 1767)	Europe	7	0	0	0	0	7
Lamiinae	Parmenini	*Parmena unifasciata* (Rossi, 1790)	Europe	3	0	0	0	0	3
Lamiinae	Phytoeciini	*Phytoecia pustulata* (Schrank von Paula, 1776)	Europe	1	0	0	0	0	1
Lamiinae	Phytoeciini	*Phytoecia nigricornis* (Fabricius, 1782)	Europe	2	0	0	0	0	2
Lamiinae	Pogonocherini	*Pogonocherus caroli* Mulsant, 1862	Europe	5	0	0	0	0	5
Lamiinae	Pogonocherini	*Pogonocherus decoratus* Fairmaire, 1855	Europe	139	0	0	0	0	139
Lamiinae	Pogonocherini	*Pogonocherus fasciculatus* (Degeer, 1775)	Europe	16	1	0	0	0	17
Lamiinae	Pogonocherini	*Pogonocherus hispidulus* (Piller & Mitterpacher, 1783)	Europe	6	0	0	0	0	6

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Lamiinae	Pogonocherini	*Pogonocherus hispidus* (Linnaeus, 1758)	Europe	55	0	0	0	0	55
Lamiinae	Pogonocherini	*Pogonocherus mixtus* Haldeman, 1847	North America	0	0	8	0	0	8
Lamiinae	Pogonocherini	*Pogonocherus ovatus* (Goeze, 1777)	Europe	19	0	0	0	0	19
Lamiinae	Pogonocherini	*Pogonocherus penicillatus* LeConte, 1850	North America	0	0	11	0	0	11
Lamiinae	Pogonocherini	*Pogonocherus perroudi* Mulsant, 1839	Europe	127	0	0	0	0	127
Lamiinae	Pteropliini	*Niphona picticornis* Mulsant, 1839	Europe	127	0	0	0	0	127
Lamiinae	Pteropliini	*Sthenias gracilicornis* Gressitt, 1937	Europe	0	3	0	0	0	3
Lamiinae	Saperdini	*Menesia bipunctata* (Zoubkoff, 1829)	Europe	2	0	0	0	0	2
Lamiinae	Saperdini	*Paraglenea fortunei* (Saunders, 1853)	Asia	0	1	0	0	0	1
Lamiinae	Saperdini	*Saperda alberti* Plavilstshikov, 1915	Asia	0	1	0	0	0	1
Lamiinae	Saperdini	*Saperda hosokawai* Hasegawa, 2017	Asia	0	1	0	0	0	1
Lamiinae	Saperdini	*Saperda octopunctata* (Scopoli, 1772)	Europe	1	0	0	0	0	1
Lamiinae	Saperdini	*Saperda perforata* (Pallas, 1773)	Europe	21	0	0	0	0	21
Lamiinae	Saperdini	*Saperda populnea* (Linnaeus, 1758)	Europe	4	0	0	0	0	4
Lamiinae	Saperdini	*Saperda scalaris* (Linnaeus, 1758)	Europe	24	0	0	0	0	24
Lamiinae	Saperdini	*Stenostola dubia* (Laicharting, 1784)	Europe	2	0	0	0	0	2
Lamiinae	Saperdini	*Stenostola ferrea* (Schrank von Paula, 1776)	Europe	28	0	0	0	0	28
Lepturinae	Lepturini	*Alosterna tabacicolor* (Degeer, 1775)	Europe	9	0	0	0	0	9
Lepturinae	Lepturini	*Anastrangalia dubia* (Scopoli, 1763)	Europe	6	0	0	0	0	6
Lepturinae	Lepturini	*Anastrangalia reyi* (Heyden, 1889)	Europe	1	0	0	0	0	1
Lepturinae	Lepturini	*Anastrangalia sanguinolenta* (Linnaeus 1761)	Europe	13	0	0	0	0	13
Lepturinae	Lepturini	*Anastrangalia scotodes continentalis* (Plavilstshikov, 1936)	Asia	0	1	0	0	0	1
Lepturinae	Lepturini	*Anoplodera rufipes* (Schaller, 1783)	Europe	5	0	0	0	0	5
Lepturinae	Lepturini	*Anoplodera sexguttata* (Fabricius, 1775)	Europe	9	0	0	0	0	9
Lepturinae	Lepturini	*Brachyleptura brevis* (Kirby, 1837)	North America	0	0	1	0	0	1
Lepturinae	Lepturini	*Brachyleptura circumdata* (Olivier, 1800)	North America	0	0	1	0	0	1
Lepturinae	Lepturini	*Brachyleptura rubrica* (Say, 1824)	North America	0	0	1	0	0	1
Lepturinae	Lepturini	*Leptura thoracica* Creutzer, 1799	Asia	0	1	0	0	0	1
Lepturinae	Lepturini	*Leptura aethiops* Poda von Neuhaus, 1761	Europe	2	0	0	0	0	2
Lepturinae	Lepturini	*Leptura aurulenta* Fabricius, 1793	Europe	7	0	0	0	0	7
Lepturinae	Lepturini	*Leptura quadrifasciata* Linnaeus, 1758	Europe	9	0	0	0	0	9
Lepturinae	Lepturini	*Neoalosterna capitata* (Newman, 1841)	North America	0	0	2	0	0	2
Lepturinae	Lepturini	*Pachytodes erraticus* (Dalman, 1817)	Europe	232	0	0	0	0	232
Lepturinae	Lepturini	*Paracorymbia fulva* (Degeer, 1775)	Europe	8	0	0	0	0	8
Lepturinae	Lepturini	*Paracorymbia hybrida* (Rey, 1885)	Europe	1	0	0	0	0	1
Lepturinae	Lepturini	*Pedostrangalia revestita* (Linnaeus, 1767)	Europe	12	0	0	0	0	12
Lepturinae	Lepturini	*Pseudovadonia livida* (Fabricius, 1776)	Europe	5	0	0	0	0	5
Lepturinae	Lepturini	*Rutpela maculata* (Poda von Neuhaus, 1761)	Europe	74	0	0	0	0	74
Lepturinae	Lepturini	*Stenurella nigra* (Linnaeus 1758)	Europe	2	0	0	0	0	2
Lepturinae	Lepturini	*Stenurella bifasciata* (Müller, 1776)	Europe	16	0	0	0	0	16
Lepturinae	Lepturini	*Stenurella septempunctata* (Fabricius, 1793)	Europe	5	0	0	0	0	5
Lepturinae	Lepturini	*Stenurella melanura* (Linnaeus 1758)	Europe	33	0	0	0	0	33
Lepturinae	Lepturini	*Stictoleptura canadensis* (Olivier, 1800)	North America	0	0	8	0	0	8
Lepturinae	Lepturini	*Stictoleptura cordigera* (Fueßlins, 1775)	Europe	203	0	0	0	0	203
Lepturinae	Lepturini	*Stictoleptura erythroptera* (Hagenbach, 1822)	Europe	1	0	0	0	0	1
Lepturinae	Lepturini	*Stictoleptura fontenayi* (Mulsant, 1839)	Europe	1	0	0	0	0	1
Lepturinae	Lepturini	*Stictoleptura maculicornis* (Degeer, 1775)	Europe	2	0	0	0	0	2
Lepturinae	Lepturini	*Stictoleptura rubra* (Linnaeus, 1758)	Europe/asia	11	1	0	0	0	12
Lepturinae	Lepturini	*Stictoleptura scutellata* (Fabricius, 1781)	Europe	29	0	0	0	0	29
Lepturinae	Lepturini	*Stictoleptura succedanea* (Lewis, 1879)	Asia	0	1	0	0	0	1
Lepturinae	Lepturini	*Stictoleptura trisignata* (Fairmaire, 1852)	Europe	7	0	0	0	0	7
Lepturinae	Lepturini	*Strangalepta abbreviata* (Germar, 1823)	North America	0	0	1	0	0	1

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Lepturinae	Lepturini	*Strangalia attenuata* (Linnaeus 1758)	Europe	1	0	0	0	0	1
Lepturinae	Lepturini	*Strangalia luteicornis* (Fabricius, 1775)	North America	0	0	4	0	0	4
Lepturinae	Lepturini	*Strophiona nitens* (Forster, 1771)	North America	0	0	3	0	0	3
Lepturinae	Lepturini	*Trachysida mutabilis* (Newman, 1841)	North America	0	0	4	0	0	4
Lepturinae	Lepturini	*Trigonarthris proxima* (Say, 1824)	North America	0	0	1	0	0	1
Lepturinae	Lepturini	*Trigonarthris subpubescens* (Kirby, 1837)	North America	0	0	3	0	0	3
Lepturinae	Lepturini	*Typocerus lunulatus* (Swederus, 1787)	Asia	0	1	0	0	0	1
Lepturinae	Lepturini	*Typocerus velutinus* (Olivier, 1800)	North America	0	0	1	0	0	1
Lepturinae	Lepturini	*Vadonia unipunctata* (Fabricius, 1787)	Europe	2	0	0	0	0	2
Lepturinae	Oxymirini	*Anthophylax cyaneus* (Haldeman, 1848)	North America	0	0	2	0	0	2
Lepturinae	Oxymirini	*Anthophylax viridis* LeConte, 1850	North America	0	0	6	0	0	6
Lepturinae	Oxymirini	*Oxymirus cursor* (Linnaeus, 1758)	Europe	4	0	0	0	0	4
Lepturinae	Rhagiini	*Anisorus quercus* (Götz, 1783)	Europe	3	0	0	0	0	3
Lepturinae	Rhagiini	*Brachyta interrogationis* (Linnaeus, 1758)	Europe	2	0	0	0	0	2
Lepturinae	Rhagiini	*Carilia virginea* (Linnaeus, 1758)	Europe	2	0	0	0	0	2
Lepturinae	Rhagiini	*Carilia virginea thalassina* (Schrank von Paula, 1781)	Asia	0	14	0	0	0	14
Lepturinae	Rhagiini	*Centrodera decolorata* (Harris, 1838)	North America	0	0	3	0	0	3
Lepturinae	Rhagiini	*Cortodera femorata* (Fabricius, 1787)	Europe	11	0	0	0	0	11
Lepturinae	Rhagiini	*Cortodera flavimana* (Waltl, 1838)	Europe	8	0	0	0	0	8
Lepturinae	Rhagiini	*Cortodera humeralis* (Schaller, 1783)	Europe	99	0	0	0	0	99
Lepturinae	Rhagiini	*Dinoptera collaris* (Linnaeus, 1758)	Europe	3	0	0	0	0	3
Lepturinae	Rhagiini	*Acmaeops marginatus* (Fabricius, 1781)	Europe/asia	3	11	0	0	0	14
Lepturinae	Rhagiini	*Acmaeops pratensis* (Laicharting, 1784)	Europe	10	0	0	0	0	10
Lepturinae	Rhagiini	*Acmaeops proteus* (Kirby, 1837)	North America	0	0	14	0	0	14
Lepturinae	Rhagiini	*Acmaeops septentrionis* (C G Thomson, 1866)	Europe/asia	24	28	0	0	0	52
Lepturinae	Rhagiini	*Acmaeops smaragdulus* (Fabricius, 1793)	Europe	6	0	0	0	0	6
Lepturinae	Rhagiini	*Evodinellus borealis* (Gyllenhal, 1827)	Asia	0	2	0	0	0	2
Lepturinae	Rhagiini	*Gaurotes cyanipennis* (Say, 1824)	North America	0	0	2	0	0	2
Lepturinae	Rhagiini	*Grammoptera abdominalis* (Stephens, 1831)	Europe	31	0	0	0	0	31
Lepturinae	Rhagiini	*Grammoptera ruficornis* (Fabricius, 1781)	Europe	266	0	0	0	0	266
Lepturinae	Rhagiini	*Grammoptera ustulata* (Schaller, 1783)	Europe	56	0	0	0	0	56
Lepturinae	Rhagiini	*Pachyta mediofasciata* Pic 1936	Asia	0	3	0	0	0	3
Lepturinae	Rhagiini	*Pachyta quadrimaculata* (Linnaeus, 1758)	Asia	0	1	0	0	0	1
Lepturinae	Rhagiini	*Paragaurotes ussuriensis* (Blessig, 1873)	Asia	0	1	0	0	0	1
Lepturinae	Rhagiini	*Pidonia lurida* (Fabricius, 1792)	Europe	3	0	0	0	0	3
Lepturinae	Rhagiini	*Pseudosieversia japonica* (Ohbayashi, 1937)	Asia	0	1	0	0	0	1
Lepturinae	Rhagiini	*Rhagium bifasciatum* Fabricius, 1775	Europe	20	0	0	0	0	20
Lepturinae	Rhagiini	*Rhagium inquisitor* (Linnaeus, 1758)	Holarctic	524	5	110	0	0	639
Lepturinae	Rhagiini	*Rhagium japonicum* Bates, 1884	Asia	0	21	0	0	0	21
Lepturinae	Rhagiini	*Rhagium mordax* (Degeer, 1775)	Europe	41	0	0	0	0	41
Lepturinae	Rhagiini	*Rhagium rugipenne* Reitter, 1898	Asia	0	4	0	0	0	4
Lepturinae	Rhagiini	*Rhagium sycophanta* (Schrank von Paula, 1781)	Europe	32	0	0	0	0	32
Lepturinae	Rhagiini	*Stenocorus cinnamopterus* (Randall, 1838)	North America	0	0	1	0	0	1
Lepturinae	Rhagiini	*Stenocorus meridianus* (Linnaeus, 1758)	Europe	71	0	0	0	0	71
Necydalinae	Necydalini	*Necydalis major* Linnaeus 1758	Europe	3	0	0	0	0	3
Necydalinae	Necydalini	*Necydalis ulmi* (Chevrolat, 1838)	Europe	1	0	0	0	0	1
Parandrinae	Parandrini	*Neandra brunnea* (Fabricius, 1798)	North America	0	0	1	0	0	1
Prioninae	Aegosomatini	*Aegosoma scabricorne* (Scopoli, 1763)	Europe	33	0	0	0	0	33
Prioninae	Macrotomini	*Prinobius myardi* Mulsant, 1842	Europe	3	0	0	0	0	3
Prioninae	Meroscelisini	*Tragosoma harrisii* LeConte, 1851	North America	0	0	236	0	0	236
Prioninae	Prionini	*Dorysthenes sternalis* (Fairmaire, 1902)	Asia	0	25	0	0	0	25

Subfamily	Tribe	Species	Origin	Europe	Asia	North America	The Caribbean	Australia	Total
Prioninae	Prionini	*Dorysthenes paradoxus* (Faldermann, 1833)	Asia	0	22	0	0	0	22
Prioninae	Prionini	*Dorysthenes* sp.	Asia	0	2	0	0	0	2
Prioninae	Prionini	*Mesoprionus besikanus* (Fairmaire, 1855)	Europe	46	0	0	0	0	46
Prioninae	Prionini	*Orthosoma brunneum* (Forster, 1771)	North America	0	0	1	0	0	1
Prioninae	Prionini	*Prionus coriarius* (Linnaeus, 1758)	Europe	4112	0	0	0	0	4112
Prioninae	Prionini	*Prionus insularis* Motschulsky, 1857	Asia	0	241	0	0	0	241
Prioninae	Prionini	*Prionus laticollis* (Drury, 1773)	North America	0	0	3	0	0	3
Prioninae	Prionini	*Prionus* sp.	Asia	0	1	0	0	0	1
Spondylidinae	Anisarthrini	*Alocerus moesiacus* (Frivaldszky, 1837)	Europe	4	0	0	0	0	4
Spondylidinae	Anisarthrini	*Anisarthron barbipes* (Schrank von Paula, 1781)	Europe	19	0	0	0	0	19
Spondylidinae	Asemini	*Arhopalus ferus* (Mulsant, 1839)	Europe	338	0	0	0	0	338
Spondylidinae	Asemini	***Arhopalus rusticus* (Linnaeus, 1758)**	Europe/Asia	4264	702	5	0	0	4971
Spondylidinae	Asemini	*Asemum amurense* Kraatz, 1879	Asia	0	5	0	0	0	5
Spondylidinae	Asemini	*Asemum striatum* (Linnaeus, 1758)	Holarctic	21	181	289	0	0	491
Spondylidinae	Asemini	*Asemum tenuicorne* Kraatz, 1879	Europe	1	0	0	0	0	1
Spondylidinae	Asemini	*Cephalallus oberthueri* Sharp, 1905	Asia	0	14	0	0	0	14
Spondylidinae	Asemini	*Cephalallus* sp.	Asia	0	3	0	0	0	3
Spondylidinae	Asemini	*Cephalallus unicolor* (Gahan, 1906)	Asia	0	15	0	0	0	15
Spondylidinae	Asemini	*Cephalocrius syriacus* (Reitter, 1895)	Europe	2024	0	0	0	0	2024
Spondylidinae	Nothorhinini	*Nothorhina punctata* (Fabricius, 1798)	Europe	2	0	0	0	0	2
Spondylidinae	Saphanini	*Oxypleurus nodieri* Mulsant, 1839	Europe	25	0	0	0	0	25
Spondylidinae	Spondylidini	*Spondylis buprestoides* (Linnaeus, 1758)	Europe	2149	8	0	0	0	2157
Spondylidinae	Tetropiini	*Tetropium castaneum* (Linnaeus, 1758)	Europe	53	8	0	0	0	61
Spondylidinae	Tetropiini	*Tetropium cinnamopterum* Kirby, 1837	North America	0	0	2	0	0	2
Spondylidinae	Tetropiini	*Tetropium fuscum* (Fabricius, 1787)	Europe	100	0	0	0	0	100
Spondylidinae	Tetropiini	*Tetropium gabrieli* Weise, 1905	Europe	166	0	0	0	0	166
Spondylidinae	Tetropiini	*Tetropium schwarzianum* Casey, 1891	North America	0	0	2	0	0	2
Spondylidinae	Tetropiini	*Tetrops praeustus* (Linnaeus, 1758)	Europe	7	0	0	0	0	7
Spondylidinae	Tetropiini	*Tetrops starkii* Chevrolat, 1859	Europe	23	0	0	0	0	23
Disteniidae	Disteniini	*Elytrimitatrix undata* (Fabricius, 1775)	North America	0	0	6	0	0	6
Vesperidae	Vesperini	*Vesperus conicicollis* Fairmaire & Coquerel, 1866	Europe	1	0	0	0	0	1
Vesperidae	Vesperini	*Vesperus strepens* (Fabricius, 1793)	Europe	6	0	0	0	0	6

In Europe, a total of 192 cerambycid species were trapped, of which seven were non-natives (three Clytini: the North American *N. a. acuminatus* and the Asian *X. chinensis* and *Xylotrechus stebbingi* Gahan; three Phoracanthini: the African *Cordylomera spinicornis* (F.) and the Australasian *Phoracantha recurva* Newman and *P. semipunctata* (F.); and one Hesperophanini: the Asian *T. campestris*). The captures amounted to about 20% of the total European cerambycid fauna (955 species, including apterous species, according to Vitali and Schmitt 2017). In North America, a total of 97 species were captured, including two non-native species originating from Europe: the Aseminii *Arhopalus rusticus* (L.) and the Callidiini *P. testaceus*. In contrast, no non-native species were trapped in Asia (95 total species), the Caribbean (12 total species; i.e. 18% of the 65 species known in Martinique; Touroult and Poirier 2021) and Australia. Three species with Holarctic distribution (the Aseminii *Asemum striatum* [L.], the Callidiini *Callidium aeneum* [Degeer] and the Rhagiini *Rhagium inquisitor* [L.]) were trapped in Europe, Asia and North America, where-

as nine species with northern Palaeartic distribution were captured in both Europe and Asia (the Clytini *Xylotrechus rusticus* [L.], the Acanthocinini *Acanthocinus griseus* [F.], the Monochamini *M. galloprovincialis* and congeners *M. saltuarius* [Say] and *M. sartor urussovii* [Fischer von Waldheim], the Lepturini *Stictoleptura rubra* [L.], the Rhagiini congeners *Acmaeops marginatus* [F.] and *A. septentrionis* [C. G. Thomson] and the Asemini *A. rusticus*).

Three species were notably abundant with captures exceeding > 5,000, including the European native *P. testaceus* (which was also trapped in the USA as a non-native species), the Palaearctic *M. galloprovincialis* (trapped in Europe and Northern China) and the Asian *X. stebbingi* which has invaded Europe. Sixteen species were represented by more than 1,000 specimens, 58 species by more than 100 specimens (Fig. 3) and 84 species by more than 50 individuals. In contrast, 109 cerambycid species from the total of 374 species were represented by only one or two specimens. More than 1,000 individuals were caught for four of the Callidiini species, of which three were native European species (*P. testaceus* – 15,126 individuals, 41 of which were trapped in North America where they have been introduced; *Pyrrhidium sanguineum* [L.]- 4,388 individuals and *Phymatodes alni* [L.]- 2,295 individuals), along with the North American *Phymatodes amoenus* (Say) (3,100 individuals).

Some invasive species were trapped in both their native range and in invaded regions (Fig. 4). The Chinese Clytini *X. chinensis* was captured in its native range around Beijing as well as in the invaded European areas in Spain, Greece (Crete) and southern France. The European species *P. testaceus* (Callidiini) and *A. rusticus* (Asemini) were

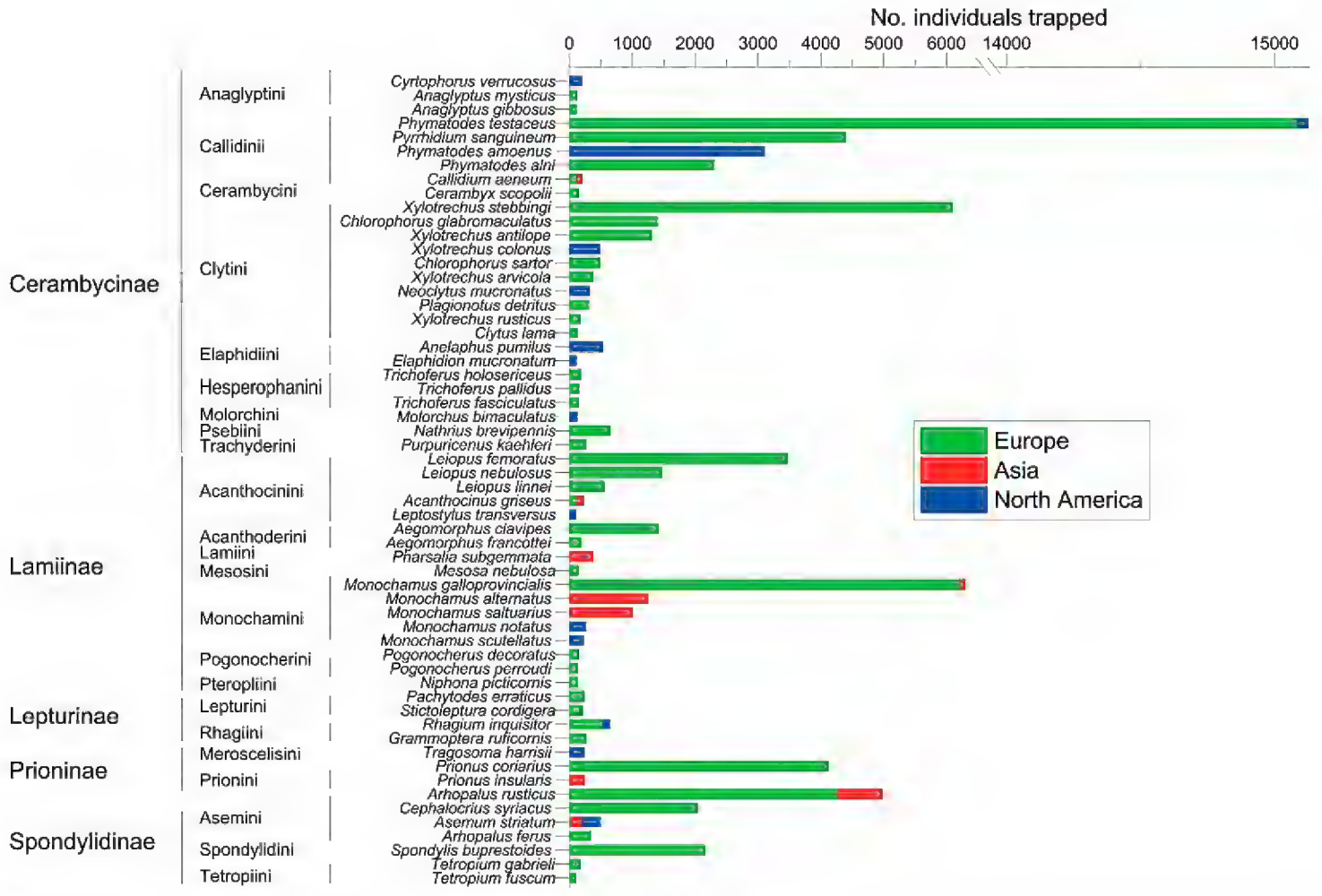

Figure 3. Cerambycid species with more than 100 inviduals captured, ranked by decreasing order and showing the continent of capture.

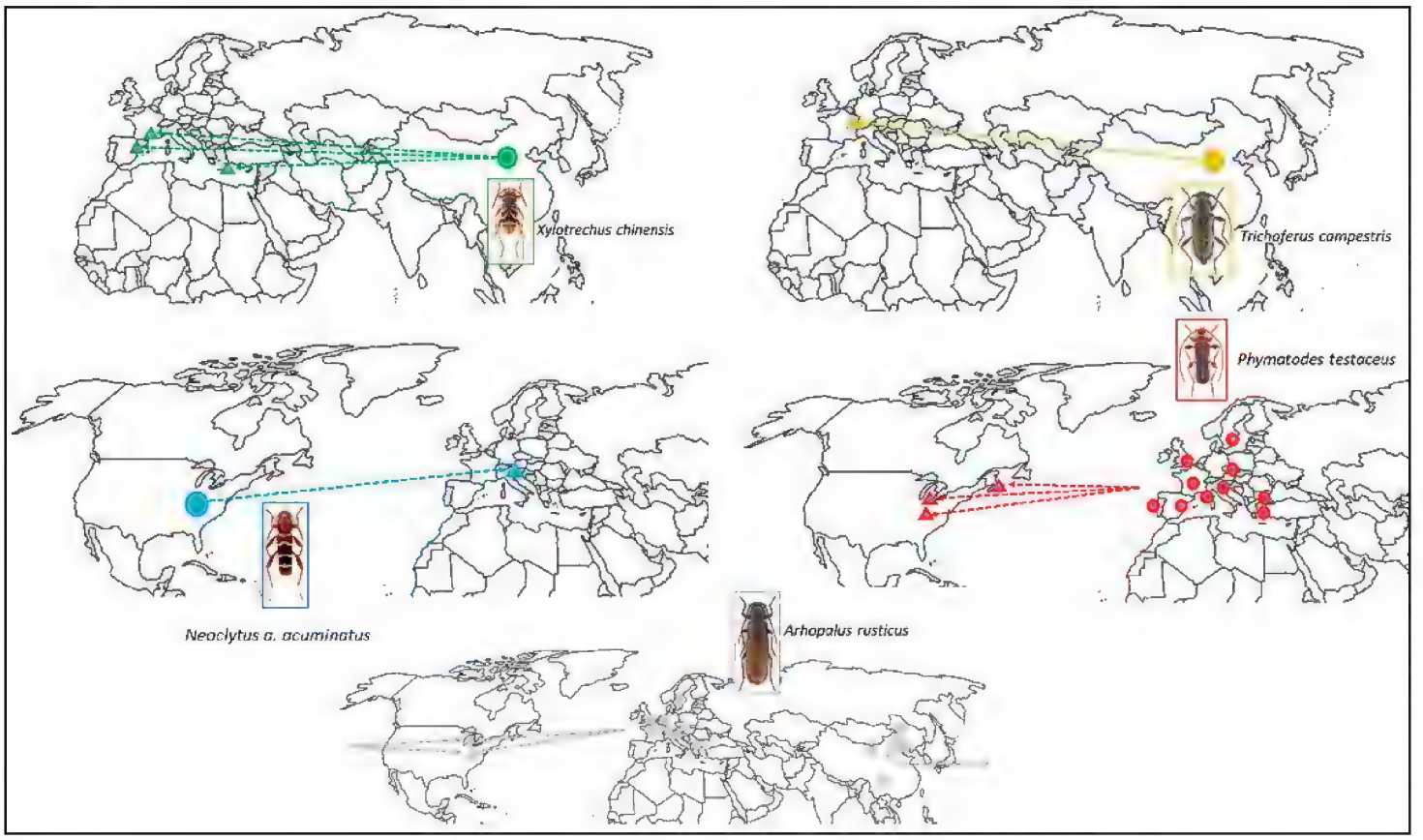

Figure 4. Cerambycid species trapped in both their native range (circles) and invaded range (triangles). Each species is shown by a different colour.

trapped in large numbers in their native Europe, but also as non-native species in North America. Conversely, the North American Clytini *N. a. acuminatus* was captured in its native range in the USA, but also in the invaded areas of Italy. A noticeable anomaly was the Himalayan Clytini *X. stebbingi*, which was caught in large numbers in southern Europe (6,089 specimens) where it is invasive, but not at all in the traps deployed in Asia. The African Phoracanthini *C. spinicornis* was regularly trapped within European ports-of-entry, but not in nearby woody areas.

Simultaneous captures of non-target Coleopteran species were mostly bark and ambrosia beetles (> 100,000 individuals), which are not yet identified to species, but also predators in the family Cleridae, essentially *Clerus mutillarius* Fabricius, 1775 (> 5,000 individuals) and *Thanasimus* spp. (> 2,000 individuals) and Trogossitidae (*Temnoscheila* spp.; > 500 individuals).

Additional captures resulting from the 10-pheromone blend

The addition of trichoferone and (*E*)-2-*cis*-6,7-epoxynonenal to the 8-pheromone blend in France and China in 2019 onwards, did not significantly change the previous trapping spectrum of the 8-pheromone blend (paired *t*-test; $P = 0.750$). However, the 10-pheromone blend resulted in trapping large numbers of four *Trichoferus* species, including the Asian *T. campestris* in its invasive range in Europe and native range in China (Table 3). In addition, large numbers of *Aromia bungii* were trapped in their native Chinese range. Only a few specimens of these five species had been previously trapped using the 8-pheromone blend.

Discussion

Capturing 376 species of cerambycid beetles from eight different subfamilies and 60 tribes on different continents, with 84 species captured in numbers greater than 50 individuals, clearly demonstrates the potential of the multi-pheromone lure to constitute an effective tool for the detection of 'unexpected' cerambycid invaders that are accidentally translocated outside their native ranges. Our hypothesis regarding the generic effectiveness of the blend was based on the evolutionary conservatism observed in many cerambycid pheromone structures. Pheromone constituents of the blend composition are shared by phylogenetically-related species on different continents (cf. references in Table 2). Therefore, their combination was expected to simultaneously attract multiple species of different tribes and subfamilies. These expected generic effects were largely supported for the targeted subfamilies, namely the Cerambycinae, Lamiinae, Spondylidinae and Prioninae.

The best represented tribe was Clytini (Cerambycinae). A total of 64 species were trapped overall, including catches in Asia (27 spp.), Europe (22 spp.) and North America (15 spp.). Two of these species were captured in both the native and invaded continents (*X. chinensis*- Asia/Europe, *N. a. acuminatus*- North America/Europe). This richness probably resulted from the presence in the blend of C6-ketol (3-hydroxyhexan-2-one) and *anti*-2,3-hexanediol. Both are known to be male-emitted attractants for a number of species in this tribe (Millar and Hanks 2017; Imrei et al. 2021). Furthermore, using these two compounds in a similar multipheromone blend in tropical China, Wickham et al. (2021) captured 26 Clytini species of which only four were in common with the present study (*Rhaphuma anongi* Gressit & Rondon, *Rhaphuma laosica* Gressit & Rondon, *Xylotrechus buqueti* [Laporte de Castelnau & Gory] and *X. chinensis*), thus suggesting an even larger potential of the blend. The Asian Clytini *X. stebbingi*, a native of the Himalayas (India, Pakistan), provides an illustrative example of the potential of detection of 'unexpected' cerambycid invaders, with a total of 6,089 specimens captured in the invaded countries of southern Europe. The species was trapped each year at more than 50 sites in southern France, Greece, Italy, Spain and Switzerland, but also in nurseries near Paris far from the invaded areas. However, it has apparently not invaded China. Somewhat surprisingly, the pheromone blend of this abundant invasive species has not yet been identified, although racemic 3-hydroxyhexan-2-one was suggested to be a key component of its pheromone (Rassati et al. 2021) and a number of other *Xylotrechus* species have pheromones comprised of 3-hydroxyalkan-2-ones, 2-hydroxyalkan-3-ones and/or 2,3-alkanediols (Millar and Hanks 2017). The richness in the trapped *Xylotrechus* species (19 spp.), a genus known to include a number of invasive species, is especially important for the early detection of new invaders.

In the same subfamily Cerambycinae, the tribe Callidiini was represented by 15 species trapped in Europe and five in North America, including a total of 11 species in the genus *Phymatodes* on the two continents. The very large number of captures (from ~ 2,000 to more than 15,000 individuals) of three *Phymatodes* species, two native to

Europe (*P. testaceus* and *P. alni*) and one from North America (*P. amoeneus*) and those of the closely-related European *P. sanguineum*, probably reflects the inclusion in the blend of both C6-ketol and 2-methylbutan-1-ol, known to be attractants for a number of *Phymatodes* spp. (Millar and Hanks 2017). Hanks et al. (2019) had previously trapped *P. testaceus* and *P. amoenus* in large numbers using these compounds, but also confirmed that the attraction to C6-ketol is antagonised by 2-methylbutan-1-ol for another species of *Phymatodes*, *P. aereus* (Newman) (Mitchell et al. 2011). Probably for the same reason, few *P. aereus* (14 individuals) were trapped during our study. A species of the Callidiini, *Callidium aeneum*, was represented by more than 200 individuals, but is another example of a species for which pheromones have not yet been identified. However, the congeners *C. antennatum hesperum* Casey and *C. pseudotsugae* Fisher are known to use C6-ketol along with semanopyrrole as their aggregation-sex pheromone blend (Millar et al. 2019). The C6-ketol compound is also likely to be a pheromone component for *Bethelium tillides* (Pascoe), a representative of another Cerambycinae tribe, Callidiopini, in Australia (Hayes et al. 2016), as indicated by our captures of *Bethelium* sp. in Australia and another Callidiopini, *C. flavus*, in Martinique.

In the subfamily Lamiinae, large numbers of individuals of 12 species of Monochamini in the genus *Monochamus* were trapped in Europe, Russia (Siberia), China and North America. This likely resulted from the inclusion in the blend of monochamol (2-[undecyloxy]-ethanol), known as a sex-aggregation pheromone for at least 14 *Monochamus* species in Europe (*M. galloprovincialis*; Pajares et al. 2010), North America (e.g. *M. carolinensis* [Olivier] and *M. scutellatus* [Say]; Millar and Hanks 2017) and Asia (*M. alternatus* Hope; Lee et al. 2018). The captures included species such as *M. sartor* (F.) and *M. sutor longulus* Pic for which no attractant had previously been recorded (but known for *M. sutor* [L.], Pajares et al. 2013). These results confirmed those obtained by Boone et al. (2018), who trapped six *Monochamus* species in North America and *M. alternatus* in Asia using monochamol. Given the importance of *Monochamus* beetles in vectoring the lethal pinewood nematode, the multilure blend would be useful for early detection of such invading species in ports and other high-risk sites. Additionally, another Monochamini in a different genus, *Uraecha angusta* (Pascoe), was trapped in China in high numbers, further indicating that monochamol is not restricted to the genus *Monochamus* Dejean.

In the subfamily Spondylidinae, Žunič-Kosi et al. (2019) recently showed that (*S*)-fuscumol, with geranylacetone as a minor component, is a sex-aggregation pheromone for a European representative of the Asemini tribe, *A. rusticus*. They also suggested that the fuscumol motif is probably shared more broadly in this subfamily. Our trapping of 15 spondylidine species supports this assumption, as the blend included fuscumol, fuscumol acetate and geranylacetone. Besides the ~ 5,000 trapped *A. rusticus* individuals, other European Asemini were captured in substantial numbers as well, including *Cephalocrius syriacus* Sharp (> 2,000 individuals), *Arhopalus ferus* (Mulsant) and *A. striatum* in Europe, but also other *Asemum* and *Cephalallus* species in China (Table 3). High numbers of captures were also noted for several species in other spondylidine tribes, such as *Spondylis buprestoides* (L.) (Spondylidini, > 2,000

individuals) in both Europe and China, for which no attractants are yet known and the alpine *Tetropium gabrieli* Weise (Tetropiini), for which Schroeder et al. (2021) recently showed an attraction to (*E*)-fuscumol.

In the subfamily Prioninae, the inclusion of prionic acid, originally identified as a female-produced sex pheromone of the North American species *Prionus californicus* Motschulsky (Rodstein et al. 2009), but also as an attractant for most, if not all, other North American species of *Prionus* (Barbour et al. 2011; Millar and Hanks 2017) and for the Asian Prionini *Dorysthenes granulosus* (Thomson) (Wickham et al. 2016a), resulted in substantial catches (> 4,000 specimens) of the European *Prionus coriarius* (L.). Additional captures of other Prionini, such as the Balkanic *Mesoprionus besikanus* (Fairmaire), the Asian *Prionus insularis* Motschulsky, and three Chinese species of *Dorysthenes* (*D. sternalis* [Fairmaire], *D. paradoxus* [Faldermann] and an, as yet, unidentified species), suggest a broad attractive spectrum for prionic acid in this tribe.

Despite the general efficiency of our blend, a number of species, especially those trapped with less than 50 individuals, are likely either random catches or were attracted by physical characteristics (e.g. trap shape and/or colour). Based on the previous results of Fan et al. (2019), who showed highly significant differences in the number of species trapped by multipheromone blends and unbaited traps, we did not deploy any unbaited control traps in this study which could help in clarifying this point. However, it is noteworthy that, very unexpectedly, we trapped a total of 79 lepturine species, including 49 in Europe, 12 in Asia and 18 in North America, although few pheromones are known in the subfamily Lepturinae and none of them, such as *cis*-vaccenyl acetate (Ray et al. 2011) or (*R*)-desmolactone (Ray et al. 2014), was included in the blend. Most of these species were caught in small numbers, consistent with random captures of individuals. Only three species (*Pachytodes erraticus* [Dalman], *Stictoleptura cordigera* [Fueßlins] and *Rutpela maculata* [Poda von Neuhaus]) out of the 44 captured in the tribe Lepturini, were represented by more than 50 individuals (Table 3). For these species, we can only speculate that the beetles were attracted to the trap colour or silhouette, rather than to the lure (see details in Cavaletto et al. 2021). Analogous results were obtained for another Lepturine tribe, the Rhaginii, where more than 600 specimens of a species considered as Holarctic, *R. inquisitor*, were caught in Europe, Asia and North America, together with the closely-related *R. japonicum* Bates trapped in China.

Attraction of these lepturines may also have been a result of the addition of high release rate ethanol and α-pinene lures to traps, rather than attraction to the blend of synthetic pheromones. Plant volatiles can, in some cases, effectively enhance the attraction of cerambycids to pheromone lures (e.g. for *Monochamus* species; Pajares et al. 2010). Indeed, plant volatiles alone, such as turpentine, have long been used as generic attractants for wood-boring insects, including some species of cerambycids, but are not as effective as pheromone-baited traps for target species. For example, Rassati et al. (2019) showed that traps deployed in Italy with a multi-lure including most of the compounds of our blend (C6-ketol, racemic 3-hydroxyoctan-2-one, *syn*-2,3-hexanediols, [*E*/*Z*]-fuscumol and [*E*/*Z*]-fuscumol acetate) caught more than twice the number of cerambycid species as ethanol-baited traps.

Our results also provide leads to possible pheromone structures in new species (see also above), building on the previously-articulated concept of "pheromone identification by proxy", in which identification of pheromones for one species may provide leads for the identification of pheromones of related taxa (Millar et al. 2019). For the 16 species caught in numbers > 1,000 individuals, it is likely that the major component(s) of their pheromones were present in the blend. Pheromones or possible pheromones had been identified from only about half of these species (*M. alternatus*, *M. galloprovincialis* and *M. saltuarius*, *A. rusticus*, *P. amoenus* and *P. testaceus*, *P. sanguineum*, *P. coriarius*, *Xylotrechus antilope* [Schönherr]; Millar and Hanks 2017). Thus, our data represent the first possible leads to the pheromone structures for a number of cerambycine species in the tribe Clytini (*C. glabromaculatus*, > 1,000 individuals), three Lamiinae in the tribes Acanthocinini (*Leiopus femoratus* Fairmaire, > 3,000 individuals; *Leiopus nebulosus* [L.], > 1,000 individuals) and Acanthoderini (*Aegomorphus clavipes* [Schrank von Paula], > 1,000 individuals) and two Spondylidinae in the tribes Asemini (*C. syriacus*, > 2,000 individuals) and Spondylidini (*S. buprestoides*, > 2,000 individuals). It is likely that the same could be true for at least some of the remaining 46 species caught in numbers > 100 individuals (and maybe even > 50), but for which pheromones have not been formally identified. For instance, Wickham et al. (2021) considered that their substantial captures of the Clytini *R. anongi* and *R. laosica* in tropical China suggested the presence of pheromone components in the blend that they tested, which was similar to ours. Our results further support this assumption because we trapped ~ 100 *R. anongi* and > 25 *R. laosica* with traps deployed at a single site of southern China.

Trapping of some invasive species in both the native and invaded ranges revealed the potential of the multilure blend for detecting invaders. Some of these non-native species have been present for a long time in the invaded areas (e.g. the European *P. testaceus* and *A. rusticus* in North America and the North American *N. a. acuminatus* in Europe). However, the trapping of very recent invaders within and near ports-of-entry is noteworthy and is indicative of the sensitivity of the blend for early detection at low population levels. For example, the Chinese Clytini *X. chinensis* was captured in its native range around Beijing, as well as in all the scattered European areas it has invaded and established in relatively recently (2013 in Spain-Catalonia; 2017 in Greece-Crete island and 2018 in southern France-Port of Sète; https://gd.eppo.int/taxon/XYLOCH/distribution/ES). Similarly, when the 10-pheromone blend including trichoferone was deployed, the Chinese Hesperophanini *T. campestris* was trapped in both its native range in China and in the river port of Huningue (France), where this invasive species had not yet been recorded. Interestingly, despite its presumably low abundance, our trapping studies allowed us to follow the dispersal of this invading species from the port. For example, in 2019 and 2020, specimens were only detected in traps placed within the Huningue Port but, in 2021, the species was captured in traps placed within a 1 km-radius from the Port. Numerous catches of *X. stebbingi* in ports-of-entry and nurseries of northern France, far from the known invaded southern area of France, also highlighted the sensitivity of the blend for its detection.

What possible improvements can be expected?

Is it possible and useful to continue increasing the number of pheromones included in the blend? The addition of trichoferone and the pheromone of *Aromia bungii* to the 8-pheromone blend in some field trials in France and China since 2020 resulted in relatively high numbers of captures of several *Trichoferus* species (three native European species and one native Chinese species invasive in Europe), as well as individuals of *A. bungii* in China, without reducing the trapping scope observed in nearby traps baited with the primary blend, especially the cerambycine *P. testaceus*. Millar et al. (2021) obtained analogous results in Pennsylvania, USA, where the responses of the major cerambycid species were not affected, except for the lamiine species *Sternidius alpha* (Say) whose catches were shut down by the addition of the pheromones of the two non-native species. Preliminary experiments (not detailed here) carried out in 2020 and 2021 in south-central France consisting of adding the sex-aggregation pheromone of *Rosalia alpina* (Linnaeus), an alkylated pyrone (Žunič-Kosi et al. 2017), to the 8-pheromone blend also resulted in captures of *R. alpina* without altering the cerambycid species richness. Tests of addition of the semanopyrrole structure (1-[1*H*-pyrrol-2-yl]-1,2-propanedione) could also be of interest, given that it occurs in pheromones of species from several continents. Wickham et al. (2016b) suggested that semanopyrrole may correspond to another well-conserved sex-aggregation pheromone motif within the subfamily Cerambycinae, being highly attractive in combination with C6-ketol for the Callidiini *Callidiellum villosulum* (Fairmaire) and as a single component for the Phoracanthini *Allotraeus asiaticus* (Schwarzer) in China. Silva et al. (2017) also identified semanopyrrole as a component of the sex-aggregation pheromone of two South American Cerambycinae in the tribe Elaphidiini, *Ambonus distinctus* (Newman) and *Ambonus electus* (Gahan). Recent work has also shown that 10-methyldodecanol, 11-methyltridecanol and their corresponding aldehydes may form another conserved structural motif, with examples of pheromones from South American (Silva et al. 2020) and North American cerambycid species (JGM and LMH, work in progress). As all these additional compounds exhibit chemical structures substantially different from the ones used in the 8-pheromone blend, it may be hypothesised that their addition will be unlikely to interfere with the attraction of species to the other eight pheromones.

For a more general approach of early detection of xylophagous invaders, targeting not only cerambycids, but also other groups, such as bark and ambrosia beetles (Curculionidae, Scolytinae), woodwasps (Siricidae) and jewel beetles (Buprestidae), represents a valuable opportunity. In fact, traps baited with some (e.g. Marchioro et al. 2020; Miller et al. 2022) or all (Cavaletto et al. 2020) the eight longhorn beetle pheromones used in this study, allowed us to catch a high number of other wood-boring beetle species and associated predators, especially when synergised by generic attractants, such as ethanol or α-pinene. The possibility of augmenting the blend with complementary attractants specific and/or generic to each of these groups is also of interest. Miller et al. (2016) already tested the combination of monochamol and α-pinene with ipsenol, a pheromone component of *Ips* bark beetles (Curculionidae: Scolytinae) and

did not observe any negative effect nor synergy on catches of Cerambycidae or on any associated species of bark beetles, weevils or bark beetle predators. However, some of the cerambycid pheromones used in the 8-pheromone blend have been shown to have either positive or negative effects on catches of bark and ambrosia beetles, depending on the species (Marchioro et al. 2020).

The position of the trap also has rather to be carefully managed. In our study, standardisation of trap position was not possible due to the different trapping locations (ports-of-entry, urban parks, forests) and the variety of environments amongst the countries included in the study. However, several recent studies have confirmed that trap position can have a considerable influence on the captures of cerambycid beetles, on a vertical gradient from the forest understorey up to the canopy (Wermelinger et al. 2007; Graham et al. 2012; Flaherty et al. 2019; Rassati et al. 2019; Miller et al. 2020; Wickham et al. 2021), as well as on a horizontal gradient between the forest edge and forest interior (Allison et al. 2019; Sweeney et al. 2020). For instance, *Monochamus maculosus* Haldeman and *M. scutellatus* were more abundant in the clearing adjacent to the forest than in the forest, whereas the contrary was observed for *M. carolinensis* and *M. titillator* (F.). As most of our field trials did not consider the upper canopy and were not deployed along forest edge-interior gradients, except for the specific 2019 experiment, it is possible that a number of species with specific types of behaviour related to these micro-environments were not trapped at all. Moreover, weather conditions during trapping periods, as well as the size of the local populations, were also likely to influence the captures.

Another important point is the colour of the trap. Most traps used in the study were black multifunnel traps (1069 out of 1289; 83%). However, Cavaletto et al. (2021), using the same 8-pheromone blend, showed that trap colour had a considerable influence on cerambycid captures in both species' richness and abundance for several subfamilies, but in different ways. For example, black traps caught significantly fewer species of Cerambycinae than yellow ones, whereas for Lamiinae, both brown and red traps caught significantly more species than black traps and colours in the portion of the visible electromagnetic spectrum (yellow, green, blue) attracted higher numbers of lepturine species than did black traps. A relationship with adult beetle behaviour could be hypothesised. Cavaletto et al. (2021) observed that the number of species of flower-visiting cerambycids was significantly lower in black traps than in yellow, blue and green ones, whereas yellow and green traps were significantly less efficient than black traps for non-flower-visiting species. Therefore, systematic tests of traps of different colours in different world regions could significantly enhance the efficiency of trapping species which respond to the multipheromone blend. Data obtained during the present study will be later merged with those of specifically-designed experiments to test for the influence of trap colour.

The impact of such trappings on local insect biodiversity could be questioned. As all specimens from non-target Coleopteran groups have not been identified yet, we cannot exclude that a few species other than cerambycids, bark and ambrosia beetles and beetle predators (clerids, trogossitids) have also been trapped in significant

numbers (> 500 ind.). However, any trapping study, like our one, is necessarily limited in scope by cost and logistical factors. Thus, unless trappings are intensively conducted over a whole region or country, which is very unlikely, they are likely to affect local biodiversity in a very limited way.

In conclusion, we are delivering a database of nearly 400 species which were trapped during the course of our multiyear field trials with the multipheromone blend, and the two hypotheses of our study are strongly supported. First, the trapping of a species in significant numbers on a continent effectively increased the probability that it can be detected upon arrival in other countries/continents, as shown by the species trapped in large numbers in both native and invaded ranges, supporting hypothesis 1. Second, the multipheromone blend was shown to be an effective generic attractant for multiple species from several cerambycid subfamilies, including numerous species for which pheromones have not yet been identified, supporting hypothesis 2. In addition, some species, such as the lepturine species caught in large numbers, were probably trapped because of trap colour or the host plant lure, rather than as a result of the blend composition. However, regardless of cues used by beetles, trapping of non-native species when they arrive at ports-of-entry has the same value for phytosanitary officials. Antagonistic effects between compounds exist, but appear to be fairly limited and so should not compromise the overall detection potential. Finally, further advances in the effectiveness of detection of cerambycids by multipheromone lures can be expected as parameters, such as trap colour and height, are optimised and as the number of pheromone components which are found to be conserved within and across related taxa and continents expands.

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Supplementary material 1

Total trapping network

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